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UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1489

Washington, D. C. ▼ November, 1927

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CORN BREEDING

By

FREDERICK D. RICHEY, Agronomist in Charge of Corn Investigations
Office of Cereal Crops and Diseases, Bureau of Plant Industry

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UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON
1927

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IMPORTANCE AND SCOPE OF CORN BREEDING

Corn is the one outstanding crop of the United States. Not only is it in a class by itself in quantity and value, but its cultivation in every State and in nearly every county makes it the preeminent American crop. With more than 100,000,000 acres in the United States annually devoted to corn, any improvement, however slight, is significant. It is for this reason that corn breeding, which may be defined as a systematic effort to improve the crop by controlling the parentage of the seed, is of the utmost importance.

The improvement sought may be in quantity or in quality. Yield generally is the chief consideration either directly or indirectly. Quality also is of importance and may be related directly to yield. Thus, the breeding of strains resistant to damage by insects reduces the damage and loss and so increases the yield of marketable corn. The development of disease-resistant strains not only reduces the percentage of moldy or rotten ears but also directly increases the yield. A study of the specific factors affecting progress in experimental corn breeding is essential to determining the fundamental principles involved. In practical breeding, however, the individual factors operating in any given environment are taken care of automatically if selection is based upon the quantity of sound grain produced under conditions of equal opportunity.

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With a better knowledge of heredity, different systems of corn improvement have been tried from time to time, and the possibilities of progress have been tested by careful experiments. It is the primary purpose of this bulletin to discuss these systems of corn breeding and consider their possibilities and limitations in agricultural practice. It is desirable to consider first, however, the underlying principles on which corn breeding is based.

PRINCIPLES OF CORN BREEDING

Any progress that may have been made in methods of corn breeding has resulted from a better knowledge of the underlying principles of genetics and cytology, achieved through intensive research not only with corn but with various plant and animal forms. Some knowledge of these principles is essential to an understanding of corn breeding. This involves a consideration of reproduction and inheritance in corn.[1]

REPRODUCTION IN CORN

The growth of corn plants from the seed is but the most obvious step in reproduction. In common with the seeds of nearly all higher plants, each kernel of corn is produced as a result of the union of sexual cells, and it is only after this union, or egg fertilization, that the different parts of the kernel develop.

THE CELL AS THE PLANT UNIT

The corn plant is built up of minute units, the cells. These differ in detail and function in different parts of the plant but are alike in general structure. Cell structure is shown in Plate 1, A and B, which are reproductions of microphotographs of tissue from the root tip of a corn seedling. Each living cell contains a specialized portion, the nucleus. If a bit of rapidly growing tissue from a corn plant is properly prepared and stained, a number of rodlike or threadlike bodies within the nuclei of some of the cells may be seen with the aid of the microscope (pl. 1, B). These are called chromosomes because of the fact that they stain a dark color with certain dyes, whereas other parts of the cell remain unstained. The chromosomes are of special interest because of their relation to inheritance.

CELL DIVISION

Growth of plant parts is due to an increase in the number and size of cells, the number being increased by the division of preexisting cells. Cell division is not a haphazard affair, but a beautifully systematic process, during which each chromosome splits longitudi-

[1] It has seemed undesirable in a general publication of this kind to attempt a detailed review of the literature of the subject. Accordingly, citations are given in the text only as direct reference is made to specific data, suggestions, or conclusions. In addition, references to publications in which more extensive lists of literature dealing with the same subject may be found are given at the end of various divisions. Mention also should be made of the many excellent texts and monographs now available on genetics, cytology, and plant breeding. These afford a far more comprehensive presentation of the underlying principles of plant and animal improvement than is possible within the scope of this bulletin. Among them may be mentioned *4*, *20*, *28*, *41*, *67*, and *71*. (Reference is made by italic serial numbers to "Literature cited," page 59.)

nally, half going to each of the two new daughter cells. All of the body cells of a plant therefore contain the same number of chromosomes. Half of these were derived from the male parent and half from the female parent of the plant at the time fertilization initiated the development of the seed from which the plant has grown.

With certain exceptions which need not be considered here, the number of chromosomes in the body cells is constant for each kind of plant or animal, the number in corn usually being 20.

As the time for reproduction approaches, certain cells in the reproductive parts of the corn plant divide in a different manner. The chromosomes become paired at this stage, one of each pair having come from the male and the other from the female parent of the plant. One chromosome from each pair, without reference to parentage, goes to one of the daughter cells, while the corresponding chromosome of each pair goes to the other. This gives rise to two

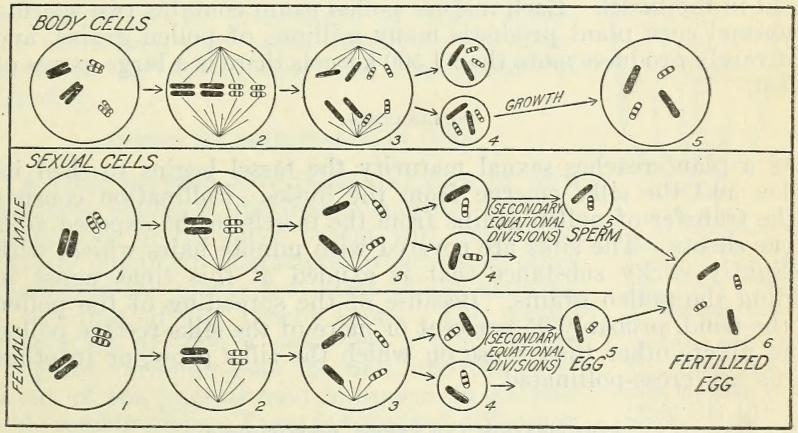


FIG. 1.—Diagram showing cell division, including both somatic (body) cell and reproductive cell formation

cells, each having half of the number of chromosomes found in the body cells. Because of the reduction in the number of chromosomes resulting from it, this is called the reduction division. Following this these cells again divide, each chromosome dividing longitudinally and half going to each daughter cell. The resulting cells, each with 10 chromosomes, are the so-called microspores or megaspores, as the case may be. The male sexual cells are derived from the microspores, and the eggs (female sexual cells) are derived from the megaspores. The steps in the formation of body and sexual cells in an organism having two pairs of chromosomes are indicated diagrammatically in Figure 1, one pair of chromosomes being shown as black and the other as crossbarred.

Every normal corn plant produces both male and female sexual cells. The former are produced in the tassel, or staminate inflorescence (pl. 2), and the latter in the ear shoot, or pistillate inflorescence (pl. 3).

THE EGGS

The eggs are located in embryo sacs within the pistils on the young cob. The pistil is made up of the silk (stigma) and a basal portion, the ovary, the wall of which after the fertilization of the egg becomes modified to form the outer layer (pericarp) of the mature kernel. (pl. 3, B.) The embryo sac is a specialized structure within the pistil and contains one egg, other cells, and two polar nuclei. All of these elements of the embryo sac originate from a single cell, the megaspore, and are qualitatively alike. Thus there is a pistil for every mature kernel that is produced, and within each pistil a single egg and two polar nuclei, the fertilization of which initiates the development of the kernel.

THE POLLEN

The sperms are formed within the pollen grains which are produced in the tassel. Each mature pollen grain contains two sperms. A normal corn plant produces many millions of pollen grains, and as it rarely produces more than 1,500 kernels there is a large excess of pollen.

POLLINATION

As a plant reaches sexual maturity the tassel begins to shed its pollen and the silks emerge from the husks. Pollination consists in the transfer of pollen grains from the tassels to the exposed silks of ear shoots. The silks are covered with minute hairs which, with a slightly sticky substance that is exuded at this time, assist in holding the pollen grains. Because of the spreading of the pollen by the wind, probably 95 per cent or more of the silks receive pollen from plants other than those on which the silks grow, or in other words are cross-pollinated.

FERTILIZATION AND KERNEL DEVELOPMENT

The pollen grain germinates soon after it becomes lodged on the exposed silk of the ear shoot. A pollen tube develops rapidly and enters the silk. It then grows down through the silk, and finally into the embryo sac, where the end is ruptured. The two sperms reach the embryo sac by means of the pollen tube. One of the sperms unites with the egg, and the other unites with the two polar nuclei. The embryo or germ develops by repeated divisions of the fertilized egg, and the endosperm is produced by the division of the nucleus formed by the fusion of the second sperm with the two polar nuclei. The endosperm constitutes all of the kernel except the embryo and the pericarp. The pericarp is developed from the ovary wall and is composed wholly of tissue of maternal origin. The different parts of the kernel are indicated diagrammatically in Figure 2.

The cells of the corn embryo normally contain 20 chromosomes, 10 of which were contributed by the sperm nucleus and 10 by the egg cell. The endosperm cells contain 30 chromosomes, 10 of which were contributed by the sperm nucleus and 20 by the polar nuclei. These

facts are of special interest in corn because of their relation to the inheritance of certain kernel characters, as will be shown later.[2]

RELATION BETWEEN REPRODUCTION AND INHERITANCE

The new plant develops from the single cell that was formed by the fusion of the egg with a sperm, and this is its only connection with the preceding generation.

The endosperm supplies the food necessary for the young plant until it has become established in the soil. It has no influence on the character of the new plant other than that exerted as a food source. The hereditary characteristics of the plant therefore must be determined by what it receives from the egg and the sperm, among which are the chromosomes.

Throughout this account emphasis has been placed upon the manner in which the chromosomes divide. The facts given are based upon actual observation and are of the utmost importance because, in connection with the observed method of inheritance of many different characters, they point clearly to the chromosomes as constituting the mechanism of heredity.

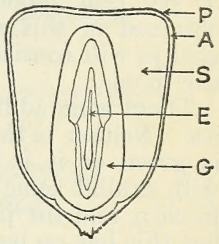


FIG. 2.—Diagram of a section through a kernel of corn showing the different parts: P, Pericarp; A, aleurone layer of the endosperm; S, starchy endosperm; E, embryo; G, scutellum. Only the pericarp (P) is formed exclusively from maternal tissue, the other parts resulting from the union of a sperm with either the egg or the polar nuclei

THEORY OF INHERITANCE IN CORN

A cross between two unlike varieties of corn produces plants in the first generation that resemble one or the other parent with respect to certain dominant characters, whereas in other characters the plants are intermediate, showing a blending of the parent types. The second generation of such a cross has a much wider range of variation than the first, and the characters of the parents tend to appear in all possible combinations. There is a marked difference, however, in the way that characters behave in transmission.

The present theory of inheritance is based upon the fundamental concept that the form and functioning of the individual is governed by definite units or factors that descend through the generations practically without change and which produce the infinite variation found in plants and animals through unlimited recombination. Some characters are differentiated by one factor, others by two or more.

There is good evidence that occasionally a factor may change or mutate. This is of much importance from its evolutionary significance but may be disregarded as relatively unimportant in its relation to practical corn breeding.

In general, both the sperm and the egg carry a full set of the inheritance factors characteristic of corn. Consequently, the fertilized egg cell and the cells of the plant formed from it contain a double set of such factors. The behavior of these factors in inheritance may be followed more readily in a typical example.

[2] Among the reports on fertilization, kernel development, and the chromosome condition in corn may be mentioned *50, 56, 58, 61, 75, 76, 77.*

INHERITANCE OF JAPONICA STRIPING IN CORN

There is a type of leaf striping known as japonica (pl. 4), and strains of corn can be obtained that breed true for this character (*53*). Other strains can be obtained that breed true for all green, or at least for the absence of this striping. If two such strains are crossed, the first generation plants, or F_1 plants as they are called, will not show the japonica character. The japonica character therefore is said to be recessive to the normal green which is the dominant condition.

If the F_1 plants are crossed with japonica, about half of the plants in the next generation will be green and the rest will be japonica. The japonica plants will breed true if pollinated among themselves. If the green plants are crossed with japonica, the result will be as before, namely, the progeny will consist of 50 per cent green and 50 per cent japonica plants. No matter how often green plants obtained in this way are mated back with japonica, the progeny always will consist of green and japonica plants in a ratio of about one to one.

There is no additive effect from the repeated inbreeding of japonica. Neither is there any intermediacy or blending. A plant either is green or it is japonica. The green plants may, and probably will, exhibit some of the many other stripings or spottings common in corn, and the japonica plants will vary in the degree of striping, but this has no bearing on the inheritance of the japonica character itself.

These are the observed facts. It is assumed that there is a single pair of factors involved. One of these, which may be called *J*, is a factor for normal pigment formation in the corn plant. The other so alters the plant processes that pigment is formed only in certain parts of the leaves, giving rise to japonica striping. This factor may be called *j*, in keeping with the custom of symbolizing a recessive factor by a small letter and its contrasted dominant factor by the same letter capitalized.

The body cells of the true-breeding green parent contained a double set of *J* and may be represented *J J*. Similarly, the japonica parent may be represented by *j j*. All of the reproductive cells of the green parent would carry only *J* and the reproductive cells of the japonica parent would carry only *j*. The fertilized eggs from which the F_1 plants were produced, therefore, would contain both the factor for normal green and that for japonica. These F_1 plants consequently may be represented as *J j*. The presence of *J* dominates that of *j* completely in this case, and the plants are green.

The reproductive cells of the F_1 plants are of two kinds. One-half carry *J* only and one-half carry *j* only. Therefore, when the F_1 plants are mated back to japonica plants the reproductive cells of which carry only *j*, two kinds of fertilized egg cells are formed, namely, *j j* and *J j*, and these are produced in equal numbers. The former will produce japonica plants and the latter green plants that are entirely similar to those of the F_1. The behavior of the factors in the case outlined is shown graphically in Figure 3.

Factors that operate as *J* and *j*, in opposition to each other as it were, are called allelomorphs of each other, and the characters they de-

termine are called allelomorphic characters. There may be any number of allelomorphs in a series, but not more than two allelomorphs can be present in a single plant. Only two factors are known in the japonica series so far, but others may exist and may be discovered at any time. If a third should be found, for example j^r, there would be three possible combinations, namely, $J\ j$, $J\ j^r$, and $j\ j^r$. As only two factors of any given pair are present in a fertilized egg cell, the presence of any one of these combinations prevents the presence of either of the others. Several series of such multiple allelomorphs are known to exist in corn. For example, R^g, R^r, r^g, r^r, and r^{ch} are concerned with the development of color in various parts of the plant, and any two of them may act as a contrasting pair (*22*).

This is known as Mendelian inheritance and is so named in honor of the Austrian monk, Gregor Johann Mendel, who first gave us the key to its principles. Mendel determined the inheritance of a number of characters in the garden pea. The same method of inheritance has been found to obtain for a large number of characters both in plants and in animals, and it is believed now that the principles apply to practically all heredity.

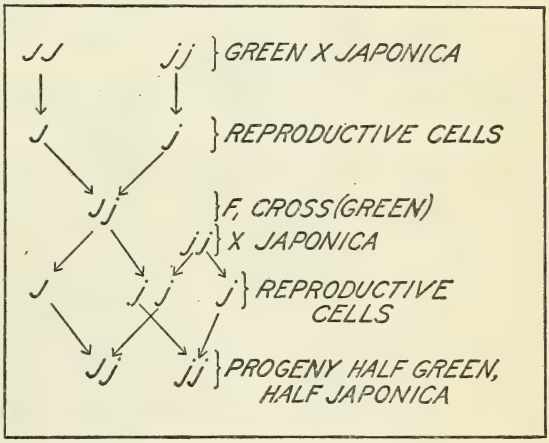


FIG. 3.—Diagram showing the behavior of a single factor pair in inheritance. A true-breeding normal green strain (*J J*) is crossed with a japonica-striped strain (*j j*). The immediate progeny are normal green (*J j*) but produce two kinds of reproductive cells *J* and *j*, as may be shown by crossing back with the japonica strain (*j j*)

Most cases are more complex than the example given. The visible characters by which inheritance is observed generally result from the interaction of a number of factors that may be inherited independently or otherwise; dominance frequently is incomplete; a single factor often, if not always, affects a number of different characters; two characters that are indistinguishable from each other in appearance may be controlled by entirely different factors; and, finally, many characters fluctuate widely in their expression as a result of environmental and other causes.

RELATION OF THE CHROMOSOMES TO HEREDITY

The theory of hereditary factors, as described, was based on evidence from a large number of inheritance studies in both plants and animals. Working from another direction, cytologists had determined the behavior of the chromosomes in cell division to be as has been outlined briefly. The similarity of the processes was so evident that the chromosomes immediately were indicated as con-

stituting the mechanism by which inheritance is accomplished. This similarity is brought out by a comparison of Figures 1 and 3. There are, however, many more heritable factors than there are chromosomes. Consequently, the chromosomes must be considered as carrying these factors, rather than as the individual hereditary units themselves.

LINKAGE

It has been shown for a number of species that the chromosomes have characteristic shapes and sizes which persist through the cell divisions and which can be identified from generation to generation. That is, the chromosomes possess individuality, and it therefore seemed probable that any given factor or factors carried by a certain chromosome at one time would tend to remain with that chromosome and that characters controlled by factors located in a single chromosome would tend to behave as a group. That this is the case has been determined experimentally.

Factors that are located in the same chromosome, as judged by their behavior in transmission, are said to be linked, and the phenomenon is called linkage. There is a tendency for linked factors to come out of a cross in the same combination as that in which they entered it in the two parents. It should not be understood, however, that linkage need be absolute. The strength of the linkage tendency differs with the individual factors.

The linkage relations of a number of factors in corn have been determined, and the phenomenon obtains here as in other species (*8*, *54*). Obviously, however, there can be as many linkage groups as there are pairs of chromosomes, and the determination of these groups is increasingly difficult as the number of chromosomes increases. It therefore is better to use an example from a form with fewer chromosomes than corn.

Because it is peculiarly adapted for the purpose, extensive genetic experiments have been carried on with the common fruit fly. This has but four chromosomes, and it has been possible for Morgan and his associates to demonstrate that the more than 300 factors for which they have determined the mode of inheritance fall within four distinct linkage groups. Moreover, the number of factors in each group corresponds to what might be expected from the relative sizes of the four chromosomes. Even more convincing is the evidence from an association of certain factors in inheritance with specific chromosomes which are concerned intimately with the determination of sex and with certain aberrant chromosome behavior. This need not be discussed here. It is enough to say that the similarity of the behavior of simple characters in inheritance to that of the chromosomes points to the latter as the mechanism of heredity, and that all evidence from more complex cases and from more detailed study supports and strengthens this theory.

INHERITANCE IN SELF-FERTILIZED LINES

Because of the importance of selection within self-fertilized lines as a method of corn improvement, it is advisable to consider also the mode of inheritance under self-fertilization. The principles are

the same in either case, as may be seen from Figure 4, which illustrates diagrammatically the segregation and recombination of a single-factor pair when a plant heterozygous for the given factors is self-fertilized.

The F_1 plants are heterozygous ($J\ j$) for japonica, but exhibit only green, inasmuch as the japonica factor is recessive. The F_1 plants form two kinds of reproductive cells in equal numbers, namely, those carrying J and those carrying j. If such a plant is self-pollinated—that is, if the silks receive pollen only from the plant on which they grow—the following four combinations will be produced in approximately equal numbers in the fertilized egg cells: (1) J ♀ J ♂, (2) J ♀ j ♂, (3) j ♀ J ♂, and (4) j ♀ j ♂. The customary symbols, ♀ for the female parent and ♂ for the male parent, have been used to indicate the factors coming in from the egg cell and sperm cell in each case. Combinations 2 and 3 are alike in so far as their effect is concerned, as it is immaterial whether a given factor comes from the male or the female parent. Consequently three kinds of fertilized egg cells or plants are produced in the F_2: (1) $J\ J$, (2) $J\ j$, and (3) $j\ j$. One-fourth of the plants in the F_2, therefore, will be homozygous $J\ J$ and will breed true for green; one-fourth will be homozygous $j\ j$ and will breed true for japonica; and two-fourths will be heterozygous, $J\ j$. The heterozygous plants are entirely similar to the F_1 plants as regards the japonica factor and if self-fertilized again will produce green ($J\ J$), green ($J\ j$), and japonica ($j\ j$) plants in the F_3 generation in a ratio of 1 to 2 to 1.

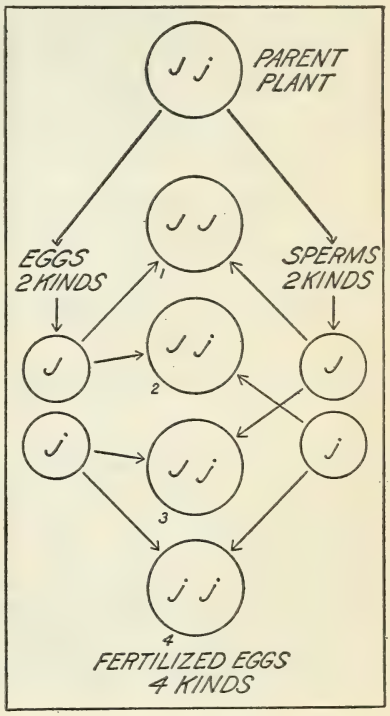


FIG. 4.—Diagram showing segregation and recombination of a single-factor pair when a plant heterozygous for the given pair is self-fertilized. The two types of reproductive cells, J and j, may come together in four different ways, and the chances for each combination are equal

This ratio is of much importance in genetic studies in determining the method of inheritance. It also is important in connection with the theory of hybrid vigor to be considered later. It should be borne in mind that in cases of complete dominance, the individuals of the heterozygous ($J\ j$) class can not be distinguished in appearance from the homozygous dominant individuals of the first class ($J\ J$). Accordingly in such cases but two kinds of individuals are apparent, dominants and recessives, in a ratio of 3 to 1. If, however, the plants are selfed (self-pollinated), the homozygous plants will breed

true, whereas the heterozygous plants will continue to segregate as did the F_1. If all of the plants in each of several successive generations are selfed, there evidently will be a much larger proportion of homozygous than of heterozygous plants in the later generations. This follows from the fact that the homozygous plants produce nothing but homozygous plants, whereas the heterozygous ones continue to produce both heterozygous and homozygous plants. The number of plants that are homozygous or heterozygous with respect to the japonica factors in six successive generations of self-fertilization, assuming equal reproduction of all classes, is shown in Figure 5. The percentage of plants homozygous for either japonica or green is shown to rise from 50 per cent in the F_2 to more than 98 per cent in the F_7 generation. This will be considered further in connection with the discussion of hybrid vigor.

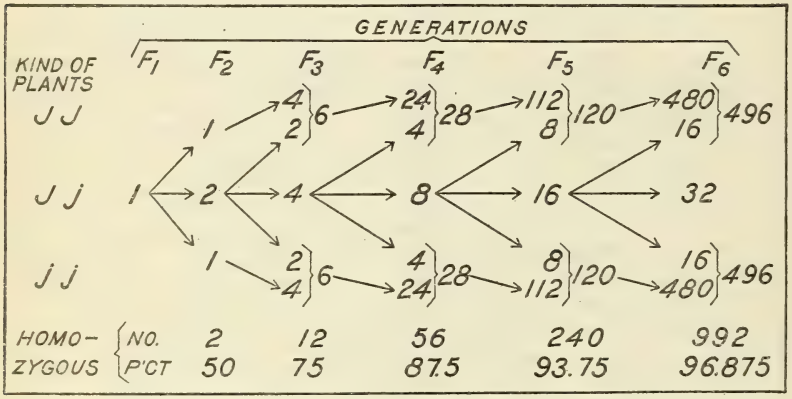


FIG. 5.—Diagram showing the proportions of homozygous and heterozygous individuals in six successive generations of self-fertilization, when the original plant was heterozygous for a single-factor pair and all classes are assumed to be propagated equally. The homozygous individuals produce only homozygous progeny, and the heterozygous individuals continue to segregate into heterozygous and homozygous progeny

XENIA

It is a matter of common observation that when white corn is grown near yellow corn the resulting ears may contain a sprinkling of yellow kernels. This is the result of partial pollination by the adjacent yellow corn. The reason for this immediate effect of pollen, or xenia as it has been called, was not understood until it was determined that the endosperm of the kernel (fig. 2) resulted from the fertilization of the polar nuclei by a sperm nucleus as already described. With this discovery it was evident that the male parent played its part in the formation of the endosperm as well as in that of the embryo, and with a further knowledge of Mendelian inheritance the behavior of kernel characters in transmission became increasingly clear (*18*, *77*).

After the reduction division, one of the cells with the reduced number of chromosomes divides equally to give rise to the polar nuclei and the egg, and these consequently are identical in so far as their chromosome content goes. The two sperm nuclei likewise are identical. It follows that the embryo and the endosperm always are

alike genetically and endosperm characters may be taken as an index of the hereditary composition of the embryo to a certain extent: This fact is of much importance in some genetic studies, as it may permit classifying the kernels before planting. Examples of xenia are illustrated in Plate 5, in which A shows the effect of partial pollination of a colorless strain by a purple strain and B shows the effect of partial pollination of a colorless sweet strain by pollen from a colorless starchy and from a purple starchy strain.

The statement that the endosperm and the embryo are identical must be made with reservations. The endosperm develops from the fusion of two polar nuclei with a single sperm nucleus. The female parent thus contributes twice as many chromosomes as the male parent in endosperm formation, instead of an equal number as in the formation of the embryo. In the case of certain endosperm characters this "double dose" coming from the female is dominant over a single dose coming from the male parent. In such cases the appearance of the endosperm is determined exclusively by the female parent and xenia does not occur. In cases of complete dominance, xenia occurs only when the dominant factor is introduced by the male parent. The inheritance of endosperm characters has been investigated intensively and affords some of the best examples of Mendelian inheritance in corn.

MULTIPLE-FACTOR INHERITANCE

As has been stated, most characters are controlled by two or more factor pairs rather than by a single pair as in the case of japonica striping. These factors are independent of one another, except for linkage, which may be disregarded here to avoid unnecessary complication. The principles are the same regardless of the number of factors involved. Each pair of factors segregates at the reduction division and recombines at fertilization to produce 1 homozygous dominant, 1 homozygous recessive, and 2 heterozygous individuals. The complexities arise from the interaction of the different factors in controlling the characters and from their recombination in a series of such 1 to 2 to 1 ratios.

INHERITANCE OF ALEURONE COLOR IN CORN

The inheritance of aleurone color in corn may be used to illustrate the possibilities of multiple-factor inheritance. The aleurone consists of a layer of cells surrounding the endosperm just inside of the pericarp (fig. 2). It is a part of the endosperm, and its character in a cross is controlled immediately by both the male and the female parents. The pigment of certain colored types of corn, notably those with reddish and purplish kernels, is formed within these cells. This color must not be confused with that of corn having red or reddish pericarps, as in red, strawberry, and bloody-butcher varieties. The pericarp is a part of the maternal tissue, as already noted, and pericarp characters therefore do not exhibit xenia.

It has been determined that at least five major factor pairs interact to determine the aleurone color of corn (*22*). Factors *A*, *C*, and *R* are necessary for the formation of red aleurone color, and as they are dominant over their respective allelomorphs, *a*, *c*, and *r*, color is formed in kernels heterozygous for these factors (*A a*, *C c*, *R r*) as

well as in those that are homozygous dominant (*A A*, *C C*, *R R*). No red develops, however, in kernels that are homozygous recessive for any one of these three pairs, regardless of the conditions of the other two. Thus, kernels of the constitution *A A*, *C C*, *r r*; *A A*, *c c*, *R R*; and *a a*, *C C*, *R R*, always are colorless because of *r r*, *c c*, and *a a*, respectively.

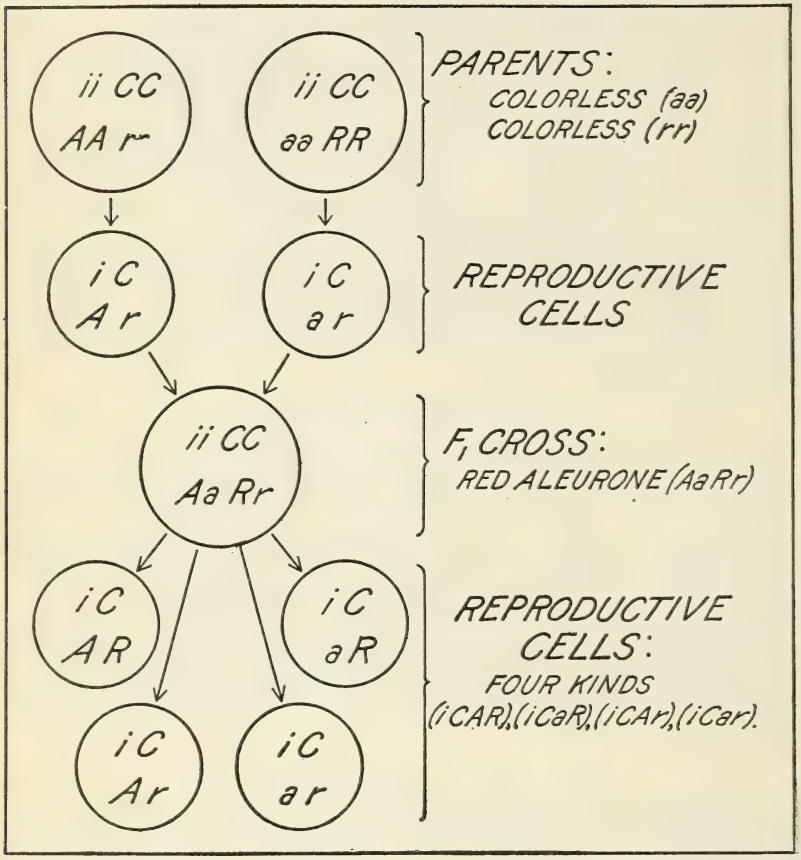


FIG. 6.—Diagram of the method of inheritance when more than one factor pair is involved. Two strains of corn with colorless aleurone are crossed. One of these (*i, i, C C, pr pr, A A, r r*) is colorless because it contains *r r*. The other (*i i, C C, pr pr, a a, R R*) is colorless because it contains *a a*. This aleurone of the F_1 cross is red, as it receives *A r* from one parent and *a R* from the other, thus being *A a, R r*. Four kinds of reproductive cells are formed in this generation, as can be determined either by appropriate crosses or by self-fertilization. The parents are both harmozygous *i i, C C, pr pr*. All of the reproductive cells therefore carry *i, C, pr*. For simplicity, *pr* is not shown in the figure

The action of *A*, *C*, and *R* as outlined in the preceding paragraph is based upon the assumption that the parents of the cross were homozygous for both *pr pr* and *i i*, the two remaining factor pairs. The factor *pr* is allelomorphic to *Pr*, which determines the formation of purple rather than red in the aleurone. *Pr* being dominant, kernels carrying *A C R* are purple if they carry either *Pr Pr* or *Pr pr*. Under these conditions, therefore, *Pr* converts what otherwise

would be red aleurone into purple aleurone. The factor pairs *A a*, *C c*, *R r*, and *Pr pr* are alike in that the dominant allelomorph of each is necessary for the development of the color.

The fifth pair of factors concerned in aleurone color formation *I i*, differs from the others in that the dominant member inhibits color, regardless of the other four factor pairs. Thus, kernels containing either *I I* or *I i* have colorless aleurone, although they may be *A A*, *C C*, *R R*, *Pr Pr*.

The behavior of two of the factor pairs, *A a* and *R r*, in a cross between colorless strains of corn is shown in Figure 6. One of the parents is colorless because it is *a a* and the other because it is *r r*. All of the F_1 kernels of the cross will have red aleurone, the necessary *A* factor being brought in by one parent and the *R* factor by the other. Actually, if *R* is brought in by the male parent the resulting kernels may be colored less deeply than if *R* comes in from the female parent, as a single dose (*R*) from the male is not completely dominant over a double dose (*r r*) from the polar nuclei. The distinction between colored and colorless aleurone is clear, however, and for the sake of simplicity the extra set of chromosomes from the female parent is not indicated in Figure 6. As both of the parent strains are assumed to be homozygous *i i*, *C C*, *pr pr*, all of the reproductive cells formed by either strain will contain *i*, *C*, *pr*, and all of the progeny will be like the parents for these factors. The *pr* factor is not shown in the figure. Its behavior is entirely similar to that of *i* or *C*.

If the F_1 generation is self-fertilized the character of the aleurone in the second generation will depend upon the way in which the four types of reproductive cells shown in Figure 6 chance to come together during fertilization. There are 16 possible combinations, and if large numbers of kernels are classified each combination will be found to occur in approximately one-sixteenth of the total number of kernels. Considering the kernels only as colored and colorless, it is immaterial whether a given factor comes in from the male or the female side, and on this basis the combinations may be grouped as shown in Table 1.

TABLE 1.—*Number of colored and colorless kernels in the F_2 generation of corn, resulting from the chance combinations of the four kinds of reproductive cells shown in Figure 6*

Group	Factors present [1]	Kernels	
		Aleurone color	Average number in every 16
a	*i i, C C, pr pr,* *A A, R R*	Red	1
b	*i i, C C, pr pr,* *A A, R r*	do	2
c	*i i, C C, pr pr,* *A a, R R*	do	2
d	*i i, C C, pr pr,* *A a, R r*	do	4
e	*i i, C C, pr pr,* *A A, r r*	Colorless	1
f	*i i, C C, pr pr,* *A a, r r*	do	2
g	*i i, C C, pr pr,* *a a, R R*	do	1
h	*i i, C C, pr pr,* *a a, R r*	do	2
i	*i i, C C, pr pr,* *a a, r r*	do	1

[1] Both parents were assumed to be homozygous for the factors indicated by the braces, and these therefore are carried by all of the kernels.

Of every 16 F_2 kernels, therefore, 9 will have red aleurone and 7 will have colorless aleurone. If the different classes are grown and continuously self-fertilized the following results will be obtained in later generations: Of the colored kernels, group a is homozygous for both *A* and *R* (*A A*, *R R*) and will produce nothing but red kernels in later generations. Group b is homozygous for *A* but heterozygous for *R r* (*A A*, *R r*). All of the progeny of this group will be *A A*, whereas the factor pair *R r* will segregate as a simple Mendelian pair into *R R*, *R r*, and *r r*, producing 3 colored kernels to 1 colorless in the F_3 generation. Group c will behave like group b, producing 3 colored kernels to 1 colorless in the F_3 generation and giving the expected simple Mendelian ratios in later generations. In group c, however, it is the *R* factor that is homozygous and the *A a* pair that is heterozygous. Group d is similar to the F_1 cross and will produce red and colorless kernels in a ratio of 9 to 7 in the F_3. Groups e, f, g, h, and i are homozygous for *a a* or *r r* or both (*a a*, *r r*). They therefore will breed true for colorless aleurone under self-fertilization or under any other system of mating that does not bring *A* and *R* into the same individual.

ALTERNATIVE AND BLENDING INHERITANCE

In the preceding analysis it was assumed that the stocks used were homozygous *pr pr*. As already noted, *Pr* converts what otherwise would be red aleurone into purple. Factors *A*, *C*, and *R* must be present if *Pr* is to have any effect, and the kernels must be *i i*, as the presence of *I* inhibits the formation of any aleurone color. It follows that if the parents in the cross considered had been *Pr Pr* all of the colored kernels would be purple instead of red.

If, on the other hand, one parent were *Pr Pr* and the other *pr pr*, the F_1 kernels would all be purple (*Pr pr*), and the *Pr pr* pair would segregate and recombine in later generations as a simple Mendelian pair. This would be independent of any segregation of the *A a* and *R r* factors.

If 64 instead of 16 kernels are taken as a basis, 36 (or nine-sixteenths) would be colored and 28 (or seven-sixteenths) would be colorless. Of the 36 colored kernels one-fourth would be purple (*Pr Pr*), two-fourths would be purple (*Pr pr*), and one-fourth would be red (*pr pr*). Accordingly the F_2 kernels would consist of 27 purple, 9 red, and 28 colorless. Here, then, we have three major color types—colorless, red, and purple—instead of two.

It has been stated that, owing to incomplete dominance, kernels receiving the *R* factor from the male parent (*r r R*) are less deeply colored than those receiving *R* from the female parent (*R R r*). This provides two classes each of red and of purple, and a more continuous series is obtained, beginning with white and extending through light red, darker red, and light purple to dark purple at the other extreme.

This is a relatively simple example of the complexities arising from the interaction of only three factor pairs affecting a single character.

Formerly it was supposed that there were two distinct phenomena of inheritance: (1) That in which two or more characters are distinct alternatives of each other with little intermediacy and (2) that

in which the characters merge into one another by more or less imperceptible stages. The former was spoken of as alternative inheritance, the latter as blending inheritance. Now, although the names are still used, it is recognized that they are merely different forms of the same thing and that there is no clear line of distinction between them. Thus, in the inheritance of aleurone color, kernels are either colored or colorless. Or, looking at it in another way, they range from colorless to dark purple. Aleurone color in corn has been chosen for discussion because it is a simple example showing the possibilities of multiple-factor inheritance. Careful analysis has shown that the inheritance of other characters that intergrade by steps so slight as to be almost imperceptible are but more complex cases of the same kind, and it now is generally believed that this is the way in which many characters are inherited.

SOME HERITABLE CHARACTERS OF CORN

The mode of inheritance has been determined for more than 60 specific factors in corn, many of which are known to affect more than a single character. Though it is beyond the scope of this bulletin to consider these in detail, some of them may well be described briefly.[3]

It should be pointed out that in describing the method of inheritance of any given character, only those factors can be considered that are known to be operative. In the case of a cross between strains having purple and white aleurone, for example, if all of the F_1 kernels are purple and the F_2 segregates into three purple to one colorless, it is known that the purple parent differed from the parent having colorless kernels by a single factor. That other factor pairs were involved could not be recognized until crossing with other material demonstrated the fact. In other words, the genetic relations determined in any case represent only the simplest conditions necessary to account for the observed facts. The evidence is positive for the action of certain factors, and the negative evidence that no other factors are involved is strengthened as each cross with unrelated strains fails to show a more complex condition. Like all negative evidence, however, this can be refuted by a single conclusive case to the contrary.

ENDOSPERM COMPOSITION

The endosperm of corn may be sugary, waxy, or starchy. In the sweet or table corns there is a much larger quantity of sugar and a smaller proportion of starch than in the field corns, resulting in the wrinkled, translucent appearance which they have when dry. The composition of the endosperm in waxy varieties differs from that of either of the preceding groups. The flint, dent, pop, and flour corns all have starchy endosperms, but they differ in the proportions of soft and horny endosperm.

Starchy and sugary kernels differ in a single-factor pair *Su su*. Starchy kernels are either *Su Su* or *Su su*, and sugary kernels are *su su*. The factor for waxy, *wx*, is recessive to its allelomorph for nonwaxy, *Wx*. Kernels carrying *su su* are sugary regardless of whether they are *Wx* or *wx*. If, therefore, starchy kernels heterozy-

[3] The mode of inheritance of a large number of factors is described in a paper published by Lindstrom in 1923 (*54*).

gous for both these pairs, *Su su Wx wx*, are planted and the plants are selfed, the following kinds of kernels will be obtained:

a------1	*Su Su Wx Wx*	9 starchy.	
b------2	*Su Su Wx wx*		
c------2	*Su su Wx Wx*		
d------4	*Su su Wx wx*		
e------1	*Su Su wx wx*	3 waxy.	
f------2	*Su su wx wx*		
g------1	*su su Wx Wx*	4 sugary.	
h------2	*su su Wx wx*		
i------1	*su su wx wx*		

Although groups g and i are indistinguishable in outward appearance and will breed true, they would give entirely different results in the segregating generations following a cross with group a. The cross between groups a and g would give a simple Mendelian ratio of 3 starchy to 1 sugary, whereas the cross between a and i again would give 9 starchy, 3 waxy, and 4 sugary in the F_2 generation (*10*). This is a good example of the way that the presence of a factor or character may remain unsuspected for generation after generation until an appropriate cross permits its expression.

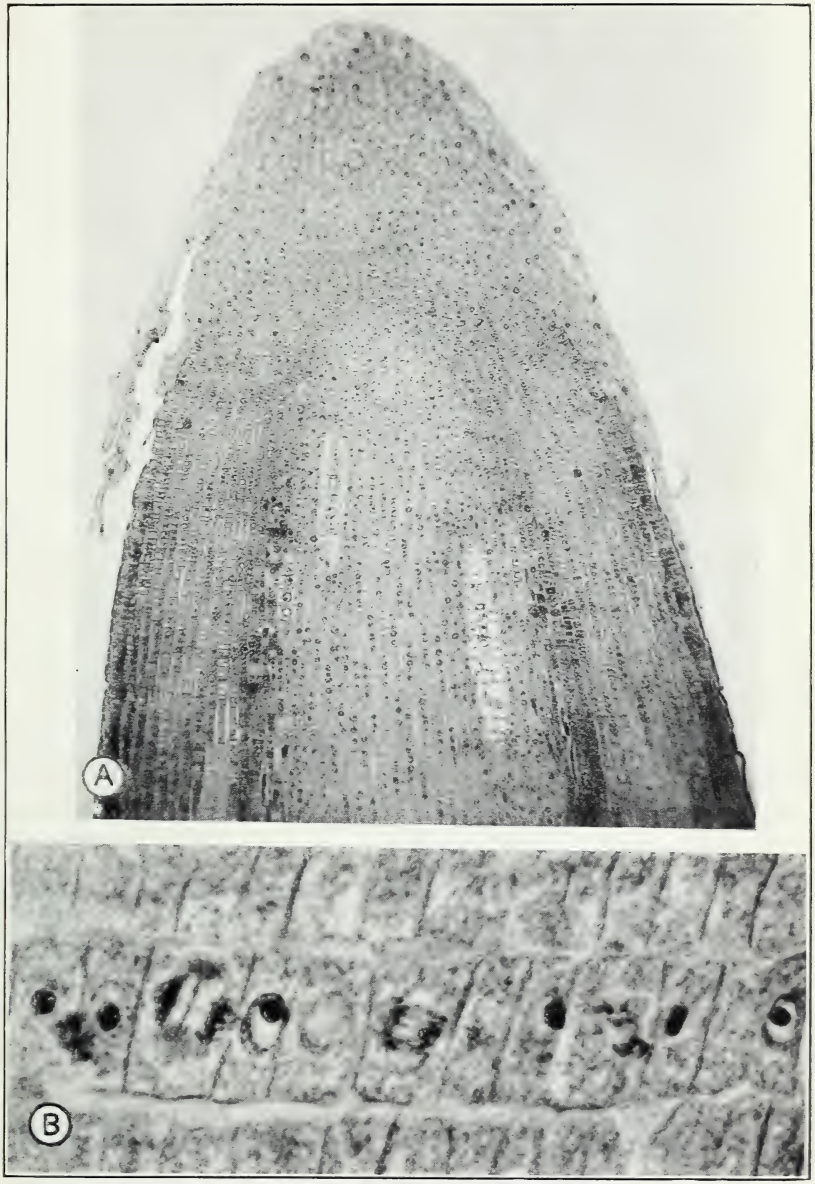
ENDOSPERM TEXTURE

Whether a starchy kernel is a flint or a flour depends upon the factor pair *Fl fl*. This is one of those interesting cases in which two doses of a factor coming from the polar nuclei of the female are dominant over a single dose of the allelomorph coming from the male parent. Thus, a true-breeding flint corn (*Fl Fl*) shows little or no immediate effect if pollinated by a true-breeding flour variety (*fl fl*). Similarly, a flour variety shows no immediate effect of pollen from a flint corn. When either of such crosses is self-pollinated the kernels segregate into 1 flinty to 1 floury, the condition being determined by the two factors from the polar nuclei without any appreciable effect from the pollen. Thus kernels having *Fl Fl Fl or Fl Fl fl* in the endosperm are flinty, whereas those with *fl fl fl* or *fl fl Fl* are floury. It should be noted that the three doses of the factor are present only in the endosperm cells, the embryo being *Fl Fl*, *Fl fl*, or *fl fl*, as the case may be (*18*).

The difference between dent and flint and between dent and flour corns is more complicated and has not been fully determined. Indentation probably is due largely to differential shrinkage while drying, the soft starch in the center of the kernel shrinking more than the horny starch around the sides of the kernel. It is influenced also by the shape of the kernels, their closeness on the ear, and other mechanical effects. Apparently there is a difference in one or more major-factor pairs, with further differences in modifying factors, making classification difficult. In general, denting is a maternal character. That is, the indentation is not immediately affected by the pollen parent, and the entire ear has about the same type of indentation. In other cases, however, the individual kernels differ, indicating that some of the minor factors may produce xenia effects.

DEFECTIVE KERNELS

A group of kernel characters closely related in their mode of inheritance to endosperm composition embraces several different types of defective kernels (*57*). Two types commonly found in corn are shown in Plate 5, C and D. These are not found in large numbers in open-fertilized corn, as they are recessive to the normal condition

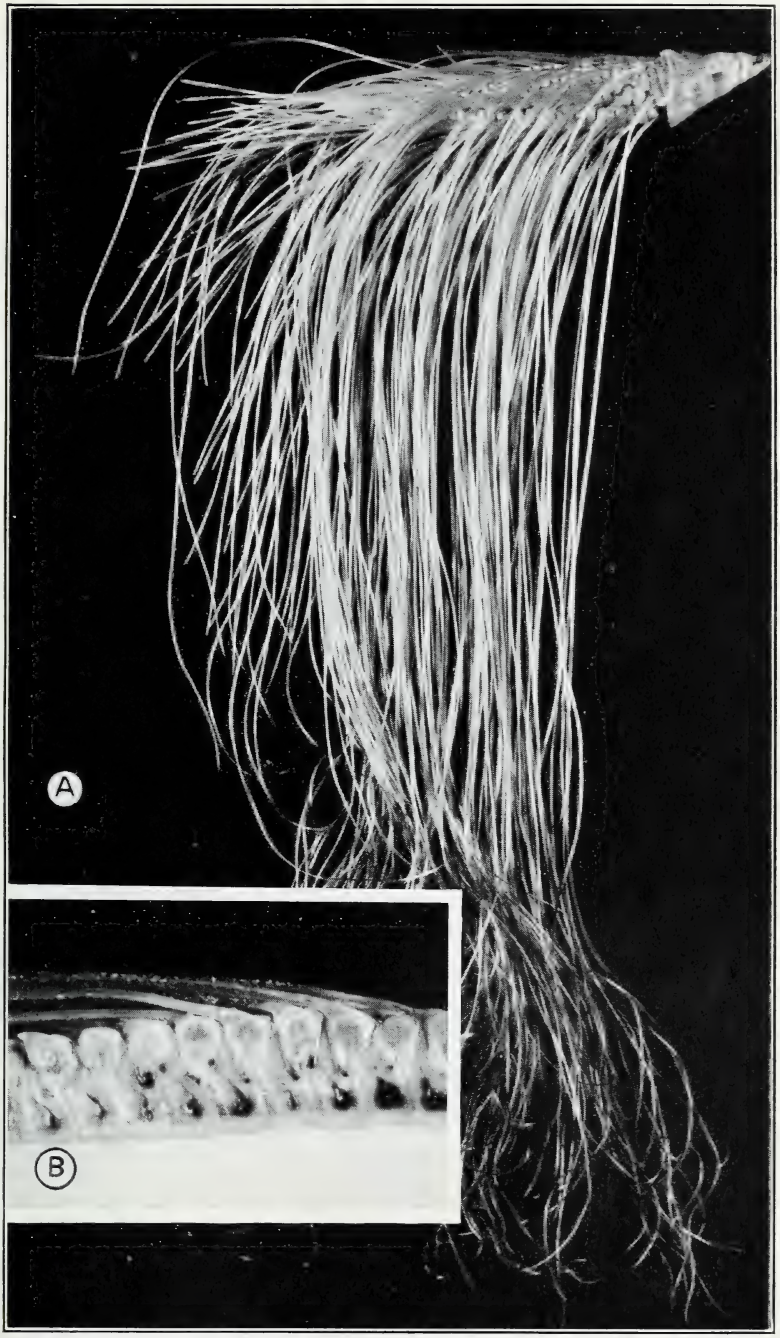


MICROPHOTOGRAPHS OF A SECTION THROUGH A ROOT TIP OF CORN

A, General structure (× 90)
B, Group of individual cells, some of which are in various stages of division (× 950)
The writer is indebted to M. N. Pope for preparing the sections and to E. G. Arzberger for making the microphotographs

THE STAMINATE OR MALE INFLORESCENCE OF CORN

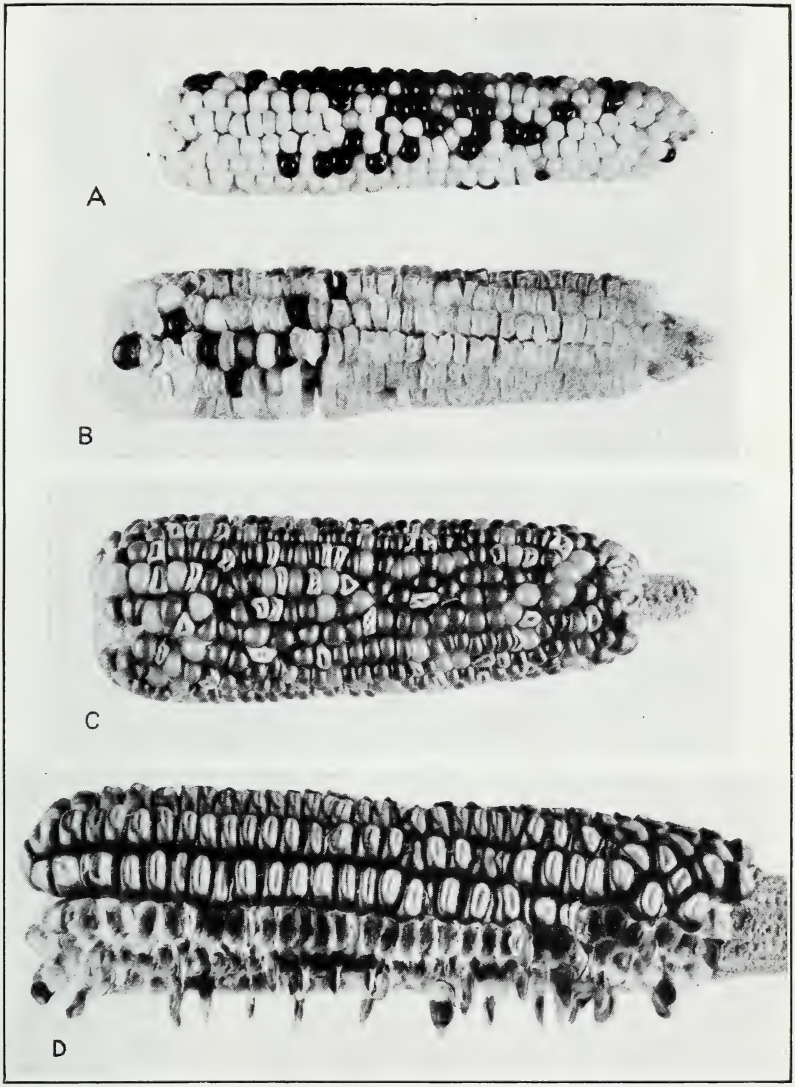
A, Complete tassel. B, A single spikelet with anthers (X7)



THE PISTILLATE OR FEMALE INFLORESCENCE OF CORN

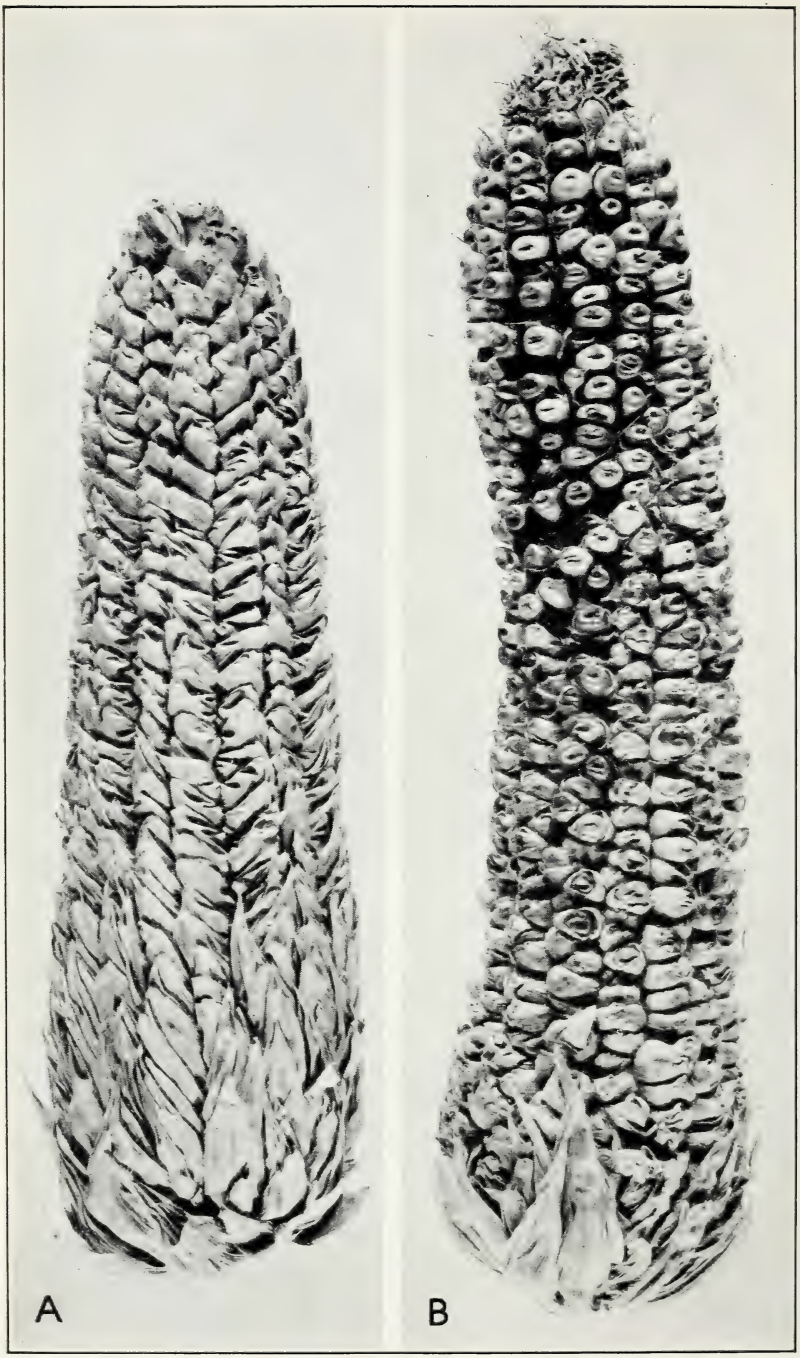
A, The young ear shoot with husks removed, showing the attachment of the silks
B, An enlarged section through a group of ovules, showing more detailed structure

A CORN PLANT SHOWING JAPONICA STRIPING



COLORED AND DEFECTIVE KERNELS OF CORN

A, Ear of white flint corn containing some purple seeds as a result of partial pollination by purple corn
B, Ear of white sweet corn with some white and some purple flint kernels due to partial pollination by white and by purple field corn
C and D, Self-fertilized ears of corn segregating for defective kernels of two different kinds



PODDEDNESS IN CORN

A, Completely podded ear. B, Kernels toward the tip decreasingly covered by the glumes

and the cross-fertilization that is common under field conditions largely prevents their expression. Close inspection of open-fertilized corn, however, shows a surprising number of ears with two, three, or more defective kernels. An idea of the prevalence of these defectives may be had from the fact that among 320 ears of a good strain of Boone County corn self-fertilized for the first time, 44 ears (13.75 per cent) had heritable defective kernels.

ENDOSPERM COLOR

There is at least one specific factor for yellow endosperm color (*Yy*). The color of heterozygous kernels is intermediate in most cases. Thus, in general, kernels with *Y Y Y* are a dark yellow, and those with *Y Y y* and *Y y y* are successively lighter. Three factors are shown in each case, because endosperm color is a kernel character in which the female parent contributes two sets of chromosomes and the male parent one. A well-known example of this fact is that yellow corn pollinated by white corn tends to be lighter than the pure yellow corn, but darker than white corn pollinated by yellow. These tendencies, however, sometimes are modified by other factors, so that they do not always hold. It seems probable from the several tones of yellow in different varieties of corn that other factors for yellow endosperm also may exist, although these tones may be due to modifying factors or to differences in kernel structure and the like. A yellow or brownish pigmentation of the aleurone cells, determined by the factor pair *Bn bn* (*51*), also occurs, which gives the kernels an appearance of having a pale-yellow endosperm.

PERICARP COLOR

The color and composition of the endosperm and the color of the aleurone may show the immediate effect of the pollen parent. The color of the pericarp or hull, on the other hand, is determined exclusively by the female parent in the season in which crossing occurs, as the pericarp is formed entirely from the tissue of the female parent. Thus, if a variety of corn with a colorless pericarp is pollinated by pollen from a variety with a red pericarp there is no evidence of this fact when the crossed ears are harvested. When planted the next season, however, all of the ears from crossed kernels will have red pericarps, and in the next generation three-fourths of the ears will have red and one-fourth colorless pericarps.

Pericarp color is controlled by the factor *P*, which is dominant to its allelomorph *p* for colorless pericarp; and just as the interaction of *J* and *j* gave three green plants to one japonica plant, so the interaction of *P* and *p* gives three plants with red ears to one having ears with colorless pericarps. There are several allelomorphs in the *P p* series which have to do with variegation of the pericarp, cob color, etc. (*2,3*). Moreover, the factor *A*, which already has been considered in connection with aleurone color, must be present with *P* if the pericarp is to be red. *P a* gives a brown pericarp instead of red (*22*).

Here again the basic facts are simple enough when each is considered separately, but become complicated in their interrelations.

CHLOROPHYLL CHARACTERS

There are several different seedling characters, some of which usually appear whenever self-fertilized corn is planted. Many of these are so deleterious that plants having them can not live beyond the seedling stage, while others are so weakening that affected plants rarely if ever mature under field conditions. Consequently they are carried only in the heterozygous condition and are not prominent in fields grown from open-fertilized seed, though some may be found in practically every field of young corn.

One of the most striking of these is the albino (white) seedling. As such an albino contains little or no chlorophyll, the green pigment by which the plant elaborates its starch, it can not live after the food supply from the seed is exhausted. One form of albino is due to the factor *w*, green plants carrying the dominant allelomorph *W* and being either homozygous (*W W*) or heterozygous (*W w*). Selfed ears throwing these albinos produce about 3 greens to 1 albino, and whether or not any are produced from ordinary seed corn depends upon the chance union in the previous generation of a sperm and an egg both of which carried *w* (*15*, *54*).

There also is a "virescent-white" type of seedling which resembles the albino at first but which soon begins to assume a yellowish green color and under favorable conditions may become entirely green and even mature its seeds. The factors concerned in this case are *V v*, virescent seedlings being *v v* and green seedlings *V V* or *V v* (*16*, *53*).

Seedlings carrying $l_1\ l_1$ in addition to either *w w* or *v v* are lemon yellow instead of white. Virescent yellow seedlings, $l_1\ l_1\ v\ v$, may become entirely green under favorable conditions and mature seeds as in the case of virescent white seedlings, $L_1\ L_1\ v\ v$. Yellow seedlings of the constitution $l_1\ l_1\ w\ w$, on the other hand, always die (*54*). Another type of yellow seedling which is distinctly deeper in color also has been reported. This behaves as a simple recessive to green, the factor pair determining its expression having been designated $L_2\ l_2$ (*55*).

The mode of inheritance for a large number of other abnormal chlorophyll types also has been determined. Some of these are apparent only in the seedling stage, others persist throughout the life of the plant, and still others appear only in the later stages of plant development. Japonica striping, the inheritance of which already has been considered, is an example of the latter condition, as the striping does not appear until the plants are six or more weeks old. Many other stripings are in this same class but need not be discussed in detail. So far as known they all are determined by one or more factors recessive to their respective allelomorphs for full green.

A large number of different leaf spottings makes up a similar group. These are more difficult of classification, and their exact mode of inheritance has not been determined as completely as in the case of the stripings. There is every indication, however, that the genetic relations in this group are largely similar to those in the other, namely, that they are due to recessive factors, the dominant allelomorphs of which are necessary for solid-green color.

With these facts in mind, it is clear that a strain of corn breeding true for all green both in the seedling and in the mature plant is homozygous for the dominant members of all of these preceding factor pairs. More than 20 such factor pairs, the recessive of any one of which will cause some type of spotting or striping, have been studied in some detail, and several others have been recognized and have been shown to be hereditary. No one of these occurs to any great extent in open-fertilized corn. There are so many of them, however, that it is difficult to find plants in open-fertilized fields that do not carry one or more types of spotting or striping, whereas in self-fertilized corn it is almost impossible. Thus, among 3,750 ears of corn of standard Corn-Belt varieties selfed for the first time, 532 (14.2 per cent) carried heritable chlorophyll defects that showed in the seedling stage (*37*). How much these may affect the vigor and consequent yield of corn is problematic. Some of the more extreme forms are very deleterious, resulting in early death or small stunted plants almost or entirely barren, and it seems logical to assume that the lesser ones also are detrimental.

Before leaving this phase of the subject it is advisable to point out that to say that these spottings and stripings are hereditary may be only part of the truth. Several symptoms are produced by an unbalanced soil solution that can not be differentiated from some of the characters that have been shown to follow hereditary lines (*31*). It therefore is probable that, in some cases at least, the condition inherited is a susceptibility or a resistance to these unbalanced conditions. In such cases the appearance of the symptoms is a result of the inherited susceptibility together with the presence of the environment necessary to their development. This, of course, is but a more complete analysis of cause and effect in these specific cases. It is an extremely helpful point of view, however, in properly weighing the importance of these abnormalities as they appear in favorable environments. Looked at in this way, some of them are but symptoms of an inherited inability to function properly rather than specifically inherited pattern factors.

DWARFNESS

Several dwarf forms are known in corn (*23*, *45*). One of these is characterized by the reduced size of all of its parts. In another the length of the internodes is the only part affected, resulting in short plants having leaves that are normal in size and number. Between these extremes are other forms, many of which are characterized by abnormalities other than dwarfness.

One form that has been named "dwarf" is conditioned by the factor pair *D d*. Normal plants are *D D* and the dwarf plants are *d d*. The latter are characterized by their very short stalks which ordinarily are not more than one-fourth as high as related normal plants. They also are characterized by other differences that need not be considered here.

Another dwarfed form, called "anther ear," also is considerably shorter than related normal plants. This form, however, is not characteristically as short as is the dwarf type. Anther ear has been shown to be a simple recessive (*an an*) to normal (*An An*).

When anther-ear plants (*an an, D D*) are crossed with dwarf plants (*An An, d d*), the F_1 plants are normal, being heterozygous for both factor pairs (*An an, D d*). In the F_2 generation, normal, dwarf, anther-ear, and dwarf anther-ear plants appear in approximately a 9:3:3:1 ratio. This is the dihybrid Mendelian ratio that would be expected, as shown below.

1 ------ *An An, D D*	9 normal.	1 ------ *An An, d d*	3 dwarf.
2 ------ *An An, D d*		2 ------ *An an, d d*	
2 ------ *An an, D D*		1 ------ *an an, D D*	3 anther ear.
4 ------ *An an, D d*		2 ------ *an an, D d*	

1 *an an, d d*=1 *dwarf anther ear.*

The point of special interest is that the dwarf anther-ear form (*an an, d d*) is notably shorter than the dwarf form (*An An, d d*), showing conclusively that the recessive factors are cumulative in their shortening effect and that size is affected by complementary factors just as are such characters as endosperm color (*23*).

PODDEDNESS

The podded condition in corn is due to the fact that the glumes, which ordinarily are rudimentary in the female inflorescence, develop and inclose each kernel in a husklike structure, giving the characteristic appearance shown in Plate 6, A. This character is of especial interest for several reasons. In the earlier classifications of corn it was made the basis for a botanical species called *Zea tunicata.* This type also has been widely advertised as "primitive corn," and it has been considered as an approach, at least, to the wild type.

The podded condition is controlled by the factor pair *Tu tu.* Normal corn is homozygous recessive, *tu tu*, whereas podded ears are heterozygous, *Tu tu.* The homozygous dominant form (*Tu Tu*) does not bear seed in the lateral inflorescence (ear), but may be propagated from seeds produced in the tassel (*11*). This statement, of course, applies to the factor pair *Tu tu*, the effect of which has been determined experimentally. It is entirely possible that a similar podded condition may be caused by some other factor pair which at the same time will permit the development of seeds on the ear.

Plate 6, B shows an ear of corn in which the podded condition decreases progressively from butt to apex. This ear is from the same parent as the one shown in Plate 6, A. Its behavior in inheritance has not been determined, and it is shown only as an example of the complexities that may occur in the inheritance of some comparatively simple characters. Characters are spoken of as controlled or determined by certain factors that segregate and recombine in this or that proportion. Such statements are entirely true in their broader sense, and it is necessary thus to reduce the problems to their simplest terms if progress is to be made. One instance of inheritance after another that seemingly was at variance with Mendelian principles has been demonstrated to come within them when carefully analyzed. It therefore seems justifiable to omit the minor complexities from consideration in general, in order to grasp more readily the broader underlying principles. It is equally advisable to stop now and then for a glimpse of the details. In few cases is inheritance

really simple. Generally it is exceedingly complex in itself and is further complicated by the variation in expression resulting from an ever-changing environment.

INHERITANCE OF PRODUCTIVENESS IN CORN

The production of grain is the final expression of all of the inherent characters of size and function, as limited by the environment in which the plants are grown. The inheritance of productiveness, therefore, must mean the inheritance of all the characters of size and function, which probably includes most if not all of the heritable characters of corn. It is a convenience in considering the inheritance of productiveness to group the characters affecting it into abnormalities, specific adaptations, and size characters. It should be kept in mind, however, that this classification is entirely arbitrary, made for convenience, and that, in general, any specific character might be placed in one group or another, depending upon the point of view.

ABNORMALITIES

Such characters as albinism and other chlorophyll deficiencies, dwarfness, heritable barrenness, and the like may be included under abnormalities. These characters are sufficiently striking to be detected readily, and their mode of inheritance can be determined in more or less detail. A number of these have been considered in preceding pages, and their importance in determining productiveness is evident. Thus, regardless of how excellent the rest of the genetic complex may be, a corn plant can produce nothing if it is barren or if it is genetically an albino and so can not live after the nutriment in the seed is exhausted. Similarly, a partial lack of chlorophyll may reduce its productiveness to a point proportional to this lack. Again, a dwarf plant attaining a height of perhaps 18 inches, with other parts proportionately small, can not equal the production of a normal plant of 8 or 10 feet; and this, too, regardless of the excellence of the rest of its heritage.

SPECIFIC ADAPTATIONS

Such characters as resistance to various disease organisms and to unfavorable conditions of soil and climate may be considered as characters of specific adaptation. The mode of inheritance of such characters is essentially the same as that of the preceding group. In fact, they differ from the so-called abnormalities chiefly in the point of view involved and in the necessity of specific conditions for their full expression. Thus, extreme susceptibility to corn smut, in connection with the presence of smut and conditions favorable to its development, may produce plants that are quite as abnormal as dwarfs. Similarly, susceptibility to one of the root rots under conditions favorable to the root rot may result in the death of the seedling just as certainly as will albinism under any conditions.

The inheritance of a number of such characters in other plants has been shown to be just as definitely Mendelian as, for example, aleurone color in corn. Because of complexities due to cross-fertilization in corn, detailed information is not so abundant regarding

their inheritance in this plant. There is ample evidence, however, to indicate that such characters as resistance to corn smut (*35*, *73*), to the root and stalk rots (*32*, *33*), to toxic soil conditions (*31*), and the like are transmitted exactly as are more obvious characters.

SIZE CHARACTERS

Striking differences in size such as those between dwarf and normal plants have been considered under "Abnormalities." The present group includes only such differences in the size of plants and plant parts as occur among ordinary plants. These differences, in general, are made up of many smaller differences each of which may be inherited independently of the others. For example, one strain of corn may be taller than another because its plants have more nodes (joints), because some or all of the internodes are longer than the corresponding ones in the other strain, or for both of these reasons. The internodes may be longer because more cells are formed, because the individual cells are larger, or because there are both larger cells and more of them. Finally, there may be more cells because cell division is more rapid, because it continues over a longer time, or because it both continues longer and is more rapid. All of these conditions are determined in their inheritance by genetic factors, some of which may be entirely independent and some of which may be interrelated. This is but a simple statement of the more obvious heritable characteristics that may affect the size of the plant. Only when it is remembered that the expression of such a complex of characteristics is limited finally by an ever-changing environment can the difficulties of analyzing size inheritance be appreciated.

In spite of these complexities, it has been possible to show by careful research that a number of size characters are inherited just as would be expected if they were determined in a manner entirely similar to that of other characters. There is no reason, therefore, for considering the inheritance of size characters as distinct from that of the other groups except as a matter of convenience (*21*).

The important point is that all of the characters of size and function that affect yield are controlled in their inheritance in the same way as are the simpler, more obvious characters of seed coloration, form, and the like. Characters affecting yield are far more complex in their interdependency and as a rule can not be dealt with individually; but fundamentally inheritance is the same: Mendelian.

HYBRID VIGOR AND PRODUCTIVENESS

The decrease in vigor and yield that follows inbreeding and the increased vigor that so frequently follows crossing have long been recognized in corn. It is only recently, however, that a satisfactory explanation of these phenomena has been forthcoming. This explanation rests upon the principles of Medelian inheritance and the fact that, in general, dominant genetic factors determine characters more favorable for growth than do their respective recessive allelomorphs.

In the preceding pages, when there was any difference between two allelomorphic characters, the character determined by the dominant allelomorph was more favorable to growth than its contrasted

recessive. Thus, for example, the recessive dwarf condition is inferior to the normal. Similarly, albino seedlings can not survive at all, whereas the condition controlled by the dominant factor allelomorphic to that for albinism produces normal plants, other things being equal. Nearly all of the known factors that determine a condition in corn strikingly unfavorable to growth are recessive to their respective allelomorphs. The same condition also obtains in large measure in other cross-fertilized plants and in animals.

It is easy to see why this should be so. Assume a homozygous strain of normal corn as a starting point. Such a strain would breed true because the two members of every allelomorphic pair would be alike. If now a mutation were to occur in some factor, the new factor (mutant) would have to be either more or less favorable for growth or indifferent in its effect. It also would have to be either dominant or recessive to its allelomorph, or dominance could be lacking.

If the new factor were dominant the character controlled by it would come into immediate expression and, if more favorable to growth, would tend to be perpetuated through the forces of natural or artificial selection. If, however, such a dominant mutant were less favorable for growth, the tendency would be to eliminate it at once. Thus, in an extreme case, if albinism were to originate as a dominant mutation, every plant carrying this new factor would be an albino which would die in the seedling stage and albinism would be eliminated from the strain.

Assume now that the mutant were recessive. It would not be expressed at all in the first generation. When it did come into expression, if it were more favorable for growth than the original factor, the tendency would be to eliminate the older factor. On the other hand, such a recessive mutant would be carried along in the heterozygous plants in which the character it controlled would not be expressed even if less favorable to growth, although there would be a tendency to eliminate it.

With intermediacy or partial dominance the tendencies would be the same in each case, but less marked. If there were little or no difference between the two factors in their effect on growth there would be no selective action, and both would tend to remain in the variety.

In the centuries during which corn has grown there has been time for innumerable mutations to occur and for selective action to eliminate such as were dominant and unfavorable to growth. Due to its extensive cross-fertilization, recessive factors could be carried along in the heterozygous condition, although when unfavorable to growth their proportion in the population as a whole would be kept at a minimum. Our present varieties of corn consequently contain an assortment of factors, some of which are more favorable and some of which are less favorable to growth. The favorable factors generally are dominant and in excess of the less favorable ones, which in general are recessive.

Such unfavorable recessives come into expression only in plants from kernels resulting from the fusion of an egg and a sperm both of which carried the specific factor. In ordinary crossbred corn this does not occur to any great extent for any one character. The total

number of unfavorable recessive characters that find expression in the ordinary corn field, however, may be quite large.

The chances are that two unrelated varieties of corn will not contain the same assortment of unfavorable recessives. Consequently, if these varieties are crossed, the cross will tend to develop according to the dominant (better) allelomorph of each pair of factors contributed by the parents. If, on the other hand, a corn plant is self-fertilized, any recessive factors for which it is heterozygous are carried in half of the eggs and half of the sperms. Many of the resulting kernels will be homozygous for one or more of the unfavorable factors carried by the parent plant. Many of the plants from inbred seeds therefore are poorly developed as a result of the less favorable characters that come into expression in this way.

A better picture of this effect with reference to a single factor pair may be had by assuming that a specific character, japonica striping, for example, is unfavorable to growth. Referring to Figure 5, it is seen that japonica striping does not appear in the cross (F_1 generation), as it is recessive. Consequently there would be no reduction in yield due to japonica in this generation. There are three normal plants to one japonica plant in the F_2 generation, and the reduction in vigor would begin. If all classes are propagated equally, the proportion of japonica plants becomes greater and greater in the succeeding generations. In the F_6 generation there are 496 japonica plants against 528 normal plants, or practically half of the entire population consists of inferior plants. The proportion of japonica plants increases quite rapidly at first, but the rate decreases in the successive generations.

The characters responsible for the more gradual decline in vigor resulting from inbreeding are less obvious in their individual effects than characters such as japonica striping and the like. They are numerous, however, and the reduction in vigor is due to the cumulative interaction of the many slightly unfavorable controlling factors. Just as the proportion of japonica plants increased most rapidly between the F_1 and F_2 generations, the rate of decrease in vigor is greatest between the first and second years of inbreeding and becomes less as stability is reached.

The facts of a decrease in vigor accompanying inbreeding and of increased productiveness following crossing are of the utmost importance in practical corn improvement. Any system of breeding that tends to bring about a narrowing of the hereditary lines gives opportunity for the expression of deleterious recessives, with a resulting tendency toward a decrease in yield. Conversely, crossing two strains or varieties tends to suppress any unfavorable recessive characters that are not common to both strains.

That crosses between varieties, strains, or selfed lines of corn usually yield more than the average of the parents and frequently yield more than the better parent is interesting evidence of the phenomenon of hybrid vigor. It is of little practical importance whenever the cross is not more productive than the better varieties already existing. The corn breeder is interested in bringing together the largest number of desirable characters into a single stock. So far it has been necessary to resort to hybridization in order to accomplish this. Hybrid vigor accordingly has been an important tool

in obtaining productiveness, but only one tool. It is of value in obtaining larger absolute yields only when the sum total of the characters expressed in the cross make it better adapted to the environment and therefore higher yielding than varieties already available.

PRACTICE OF CORN BREEDING

Corn breeding has been defined as a systematic effort to improve the crop by controlling the parentage of the seed. The control of the parentage is exercised in practice by selection, and the different systems of breeding for increased yield will be considered, according to the methods of selection followed, under the headings of mass selection, ear-to-row selection, hybridization, and selection within selfed lines. Corn breeding usually has as its objects an increase in the acre yield of marketable corn. The discussion, therefore, will be concerned primarily with attempts to increase the yield by selection for general vigor, productiveness, and quality. Breeding for resistance to some specific disease or condition is but a special application.[4]

MASS SELECTION

Mass selection consists in picking out certain individuals from the main crop and planting the selected seed en masse. With corn, selection may be on the basis of the ear only, or on the basis of the plant and the ear. In the former case the ears most nearly approaching the ideal in mind are chosen without reference to the plants on which they grew. In the latter case selection takes place in the field, and primary importance is attached to the character of the plant on which the selected ear is produced.

Because of the large size of the seed units—the ears—some degree of mass selection has been practiced by corn growers since the earliest times. Indeed, it is probable that long before the coming of the white man to America the Indians had selected their seed ears on the basis of some character or other. It generally is conceded that this selection has been of the utmost importance in improving corn and adapting it to the varying conditions under which it is grown. There also is ample evidence that varieties may still be adapted to new environments or may be modified in this or that character by mass selection.

Because of the cross-fertilization that regularly occurs in corn, modification by mass selection is a shifting of the average rather than a true fixation of type. Even the most intensively selected varieties of corn are only mixtures of hybrids which, within limits, can be modified practically at will by selection. It is for this reason that varietal names mean practically nothing in corn.

SELECTION FOR EAR TYPE

The ideas of the earlier corn breeders differed widely as to what constituted the best type of ear. This is shown by such varieties as

[4] Much of the earlier literature on the results of experimental corn breeding was reviewed by the writer in a previous publication (*62*). More recent publications which should be mentioned and to which specific reference is not made in the text are *13, 14, 24, 26, 29, 46, 47, 59, 65,* under "Literature cited," p. 59.

Reid, Leaming, Hickory King, and the small-eared prolifics, the characteristics of which illustrate differences in the ideals of the breeders who established them (pl. 7). Some growers even believed that it was undesirable to select for a specific type and made it a point to include choice ears of different kinds in each year's selection.

With increasing competition at corn shows, standards for judging the exhibits became desirable, and the judges formulated a set of such standards for their guidance at the exposition in Chicago in 1886. Orange Judd prepared a score card for the Illinois State Fair at Peoria in 1891, which was modified and adopted later by the Illinois Corn Growers' Association. Once conceived, the idea was quickly adopted in other States, and the result was the corn score card.

In all probability seed value was not the important point at issue in these earlier corn shows. That is, a farmer's ability to produce a fine corn crop by the use of good soil, good seed, and good cultivation was measured by the sample of the crop, not seed, that he showed. As early as 1895 Plumb noted that such a score card "has no more value than a scale of points in judging butter, where the breed of cow and her profitable character are not considered" (*60, p. 56*). Nevertheless it was but natural to assume that seed selected on the same basis would produce increased yields. Accordingly, much attention was devoted to score-card selection. The progress was not all that had been anticipated, and experiments were undertaken to determine what relation there was between the physical characters of seed ears and yield.

Seed ears differing in specific characters have been compared experimentally many times. Slight differences have been found between the yields of the various types, but these were too small to be of much significance in any one experiment. The conclusion of investigators has been practically unanimous that the slight physical differences among good seed ears are of no value in indicating their relative productiveness.

Detailed results now are available covering a large number of comparisons for certain characters that have been studied most extensively. When these are considered as a whole, certain trends are apparent. Thus, a majority of the comparisons of ears of different weights are in favor of the heavier ears, in spite of the fact that, in general, all of the ears compared were suitable for seed and therefore above the average weight for the variety. The comparisons also indicate, in general, that ears which are heavy because they are long are likely to be more productive than those which are heavy because of a large circumference. Finally, the evidence points to ears with heavier cobs, fewer rows, fewer kernels per inch, and a lower shelling percentage and smoother indentation than the old standard show type, as being the better yielders.

It has been shown that extremely rough, starchy ears are more susceptible to the rot diseases of corn than the smoother, more flinty type which is indicated as being more productive in the comparisons referred to (*32, 74*). Better maturity and resistance to disease consequently may have been the reasons for the slight superiority of the smoother type. In any event, so far as there is any difference in yield, the evidence favors ears more like that shown in Plate 8, A, than like the so-called "pretty ear" shown in Plate 8, B, with nicely

rounded butt, well-filled tip, and a high percentage of shelled grain. The further considerations of quality and disease resistance also warrant selection toward the longer, smoother ear, with fewer rows of kernels and thicker kernels.

There is some evidence that too close selection for any given kind of ear may reduce yields by bringing about a condition approaching that produced by inbreeding (*25*). The best plan, therefore, appears to be to select sound, well-developed ears of an adapted variety without trying to make them conform to any very specific type.

SELECTION FOR PLANT TYPE

There seem to be no characters of the corn plant that can be classed as uniformly advantageous from the standpoint of yield, except those indicating normal vigorous development. Thus, larger, leafier plants may be more productive in one environment, and smaller, less leafy plants may be better under other conditions. In other words, the question is one of adaptation rather than of specific form or function, and selection should be toward the kind which is adapted best to the conditions under which the corn is to be grown.

A possible exception to this is the tendency to produce more than one ear per plant. A number of experiments have shown that prolific strains, i. e., those having a strong tendency to produce more than one ear per plant under fairly good conditions, are inclined to be more productive than similar strains that normally produce but one ear per plant (*6*, *52*). The best evidence for this comes from comparisons in the Southern States, where a long growing season permits larger yields from the individual plants. The flint and flour varieties of the North, however, also tend to have more than one ear per plant and are extremely efficient in producing grain under adverse conditions. The ears are smaller in prolific varieties, and the methods of handling the corn crop in the Corn Belt have not been conducive to developing adapted prolific sorts. Consequently, there is little evidence as to the value of selection for prolificacy in this region. With an increased use of mechanical corn pickers such varieties may be developed, and the evidence from other sections indicates that they should be more productive than single-eared varieties. The lack of experimental evidence on this point at the present time, however, prevents an unqualified recommendation to select for more than one ear per plant in the Corn Belt.

PLACE OF MASS SELECTION

The development of practically all of our present varieties of corn was achieved by mass selection, and, although progress with this method is slow after grosser adaptation has been achieved, there is every evidence that it is effective in at least maintaining yields. Mass selection unquestionably is the only method of corn improvement to be recommended for the average individual who does not have specific training in plant breeding. More elaborate methods will be discussed, but their practice will be restricted largely to technical plant breeders working at experiment stations, with large seed growers, or with farmers' cooperative associations of one kind or another.

Seed ears should be selected in the field before husking, from normal, vigorous plants that have produced sound, well-developed ears. Plants showing any evidence of disease, such as corn smut or the ear, stalk, and root rots, should be carefully avoided. The specific type of ear and plant is unimportant if selection is toward a kind that is adapted to the environment in which the crop is to be grown. The selection of unadapted types, such as large ears from late-maturing plants for conditions requiring smaller ears and earlier maturity, or plants that mature too quickly to utilize the full available growing season, and the like, is the thing to be avoided.

EAR-TO-ROW SELECTION

Breeding corn by ear-to-row selection was introduced by the Illinois Agricultural Experiment Station about 1896. It became popular almost immediately and soon was in wide use. Ear-to-row selection consists in planting the seed from each of a number of ears in individual rows and basing selection on the performance of these rows. That is, each row is harvested separately, the yield and quality of product is determined, and seed is selected from the better and more productive ear rows for continued selection and is multiplied for general planting.

Fundamentally, then, ear-to-row breeding is based upon the principle that the measured ability of the seed on a selected ear to produce a crop of large size or specific character is evidence of the value of that ear for breeding stock. The exact method of applying this principle differs according to the means used (1) to overcome the influence of variation in the productivity of the soil on the indicated value of the different ears and (2) to obtain seed for continued selection and for general planting.

It was recognized that differences in the productivity of the soil from row to row frequently were more important in determining the yield of the various rows than were the inherent differences among the individual seed ears. Thus, a row from an ear that potentially was unproductive might yield well because of the soil in which this row grew. On the other hand, an ear row which should have yielded well might yield poorly because it occurred in an unproductive part of the plat. Two methods were used to overcome this effect of soil variation. A mixture of seed was planted in rows distributed at regular intervals among the rows of the ear-to-row plat. These check (or control) rows were harvested in the same way as the ear rows, and their yields were used as a measure of the productiveness of the different parts of the plat. The other method of eliminating the effect of soil variation was to plant the seed from each ear in two or more rows in different parts of the plat instead of in one row. The average yield of two or more separate rows from the same ear is more likely to represent the true value of that ear for breeding stock than is a single row. The use of check rows, or replication, or both, became general in an effort to make the results of the ear-to-row plat a more reliable basis for selecting the productive ears. The length of row, number of replications, and frequency of check rows were details that differed with the individuals practicing this method of selection and need not be considered.

Under what may be called the direct method of ear-to-row selection, the plat is gone over every day or every other day during the tasseling period and alternate halves of alternate rows are detasseled. Thus, the tassels are pulled from the plants in one end of rows 1, 3, 5, etc., and from the plants in the other end of rows 2, 4, 6, etc. The tassels are pulled as soon as possible after they appear, and before they begin to shed pollen. Just before harvest the better ears from the better detasseled plants in each row are picked for possible use as seed, the ears from each row being kept separate. The plat is then harvested and the yield of each row determined. The best 6 to 10 ears from detasseled plants in the 10 to 15 more productive rows are used for the next year's ear-to-row plat. The other seed ears from the more productive rows are shelled together and the seed used to plant a multiplying plat from which seed is selected for general planting.

Under the remnant method the ear-to-row plat is a test plat in which to determine the relative value of the different ears. Only a part of the seed from each ear is planted in this plat. The remnant seed of the few best ears then is used for planting a multiplying plat the following year. The remnant seed of the one to three highest yielding ears is used to produce pollen-parent plants, the seed from the second-best producing ears being used to produce pistillate-parent plants. These two lots of seed are planted in such a way that there will be one row of pollen-parent plants alternating with one, two, or three rows of pistillate-parent plants. The latter are detasseled before they shed any pollen, so that the seed produced on them is pollinated by pollen from the pollen-parent plants. Only the seed from the detasseled plants is used for general planting, ears being selected from the general field for another ear-to-row plat.

RESULTS OF EAR-TO-ROW SELECTION

As already noted, ear-to-row corn breeding came into immediate prominence. The method seemed fundamentally sound. The earlier results showed wide differences in the productiveness of the seed from different ears. Later, the yield of seed from high-yielding ear rows was shown to be larger than that from low-yielding ear rows or from mass-selected seed. As a consequence nearly all of the agricultural experiment stations and many seedsmen and farmers took up ear-to-row breeding.

TABLE 2.—*Average oil and protein content of corn of four selected strains and of the parent variety in Illinois*

[Data from the Illinois Agricultural Experiment Station (*28, p. 193–194*)]

Designation of variety and strain	Years	Oil content	Protein content
		Per cent	*Per cent*
High-oil strain	1911 to 1915	8.02	----------
Low-oil strain	do	2.03	----------
High-protein strain	do	----------	14.53
Low-protein strain	do	----------	7.74
Burr White (parent variety)	1896	4.70	10.92

The success of the now classical experiments on selection to modify the chemical composition of the corn kernel conducted at the Illinois Agricultural Experiment Station had an important influence in promoting acceptance of the principle of ear-to-row corn breeding. Beginning in 1896 with Burr White corn, selections were made by the ear-to-row method for high-oil and low-oil and for high-protein and low-protein content. The effects of this selection on the four strains isolated are shown in Table 2.

In spite of the evident success of these experiments in modifying the chemical composition of the corn kernel and the earlier indications of larger yields obtained by similar methods, later experiments covering a longer period have failed to show that ear-to-row selection was successful. That is, there has been no evidence of a cumulative increase in yield under continuous ear-to-row selection. True, most of the experiments have continued to show progeny seed from high-yielding ear rows to be more productive than progeny seed from low-yielding ear rows. The differences have not been large, however, and in some experiments became less rather than more as ear-to-row selection was continued. Data from experiments at the Nebraska Agricultural Experiment Station are shown in Table 3, as an example of the results of ear-to-row selection by different systems. These show no significant increase in yield from any of the more elaborate methods of breeding over those obtained by simple mass selection as represented by the original Hogue Yellow Dent and Nebraska White Prize varieties.

TABLE 3.—*Yields produced by mass-selected seed of two varieties of corn and by strains obtained from these varieties by ear-to-row selection in Nebraska*

[Adapted from Kiesselbach (*48, p. 106, 109*)]

Designation of variety and strain	Acre yields of shelled corn (bushels)											
	1911	1912	1913	1914	1915	1916	1917	1920	1921	Average		
										1911–1917	1913–1921	1915–1921
Original Hogue Yellow Dent	42.6	51.6	9.8	62.8	79.5	71.7	57.4	------	------	53.6	------	------
Continuous ear-to-row selection since 1903	44.0	52.9	7.7	65.3	76.8	69.8	56.6	------	------	53.3	------	------
Increased from single strain selected in 1906	38.2	45.6	7.3	55.0	75.3	58.9	53.6	------	------	47.7	------	------
Increased from composite of four strains selected in 1906	42.5	54.6	12.1	63.5	80.0	74.4	57.9	------	------	55.0	------	------
Intercrossing of four strains selected in 1906	41.6	55.3	9.1	64.7	84.1	69.4	57.3	------	------	54.5	------	------
Original Nebraska White Prize	------	------	10.0	52.3	75.5	73.8	48.2	52.4	68.6	------	54.4	63.7
Continuous ear-to-row selection	------	------	10.4	50.0	72.2	73.0	46.8	55.7	68.5	------	53.8	63.2
Composite of best eight strains	------	------	12.3	49.0	71.6	72.5	47.7	47.0	64.6	------	52.1	60.7
Intercrossing of strains	------	------	------	------	73.7	74.1	47.9	59.1	69.4	------	------	64.8

As an example of results more favorable to ear-to-row breeding, data from the Ohio Agricultural Experiment Station are shown in Table 4. In these experiments the remnant seed of the parent ears of the four or five highest yielding ear rows of one season was used

to plant a crossing block the next season. Pollen-parent plants were from the ear indicated by the ear-to-row test as most productive, and pistillate-parent plants were from the second-best ears. In all, each of 20 crosses were compared for periods of from one to three years. Of these, 18 were more productive and 2 were less productive than field-selected seed. The averages of the three to four crosses tried each year were more productive in every case, the average increase during the eight seasons covered being 5 bushels per acre. This increase was from the immediate progeny of the productive ears. How much of it would persist in later generations is not clear.

TABLE 4.—*Comparative yields of strains of corn selected by the ear-to-row method in Ohio*

[Adapted from Williams and Welton (*78, p. 99*)]

Group	Strain No.	Years grown	Average acre yields for years grown (bushels)		
			Selected strain	Check	Increase above (+) or decrease below (−) check
No. 1	41	1907 and 1908	77.45	79.43	−1.98
	42	do	84.41	79.43	+4.98
	43	do	83.68	79.43	+4.25
No. 2	95	1909, 1910, and 1911	80.67	74.43	+6.24
	96	do	82.67	74.43	+8.24
	97	do	81.74	74.43	+7.31
No. 3	202	1910 and 1911	64.72	61.04	+3.68
	203	do	66.24	61.04	+5.20
	204	do	62.51	61.04	+1.47
	205	do	69.57	61.04	+8.53
No. 4	315	1911 and 1912	88.62	80.44	+8.18
	316	do	82.21	80.44	+1.77
	317	do	83.03	80.44	+2.59
No. 5	651	1913	84.16	79.03	+5.13
	652		82.60	79.03	+3.57
	653		78.91	79.03	−0.12
No. 6	803	1914	79.84	73.60	+6.24
	804		77.37	73.60	+3.77
	805		84.60	73.60	+11.00
	806		81.22	73.60	+7.62

The results of selecting for high and for low yield by the ear-to-row method at the Illinois Agricultural Experiment Station are of special interest (*72*). The experiment was begun in 1911 with a foundation stock of 990 ears. Seed of these ears was planted an ear to a row, and a composite lot of seed representing all 990 ears was planted in an isolated plat. This composite lot of seed constituted the foundation stock for a nonpedigreed strain that was propagated by simple mass selection.

High-yield and low-yield selection plats of 40 ear rows each were planted in 1912 and subsequently. The remnant seed of the 40 highest producing and the 40 lowest producing ears in the 1911 test was planted in 1912. After that, seed for the high-yield plat was selected from the 10 highest yielding rows of the preceding year's high-yield plat, whereas seed for the low-yield plat was selected from the 10 lowest yielding rows of the preceding year's low-yield

plat. In both cases seed was selected only from detasseled plants of the selected rows and from the better available plants.

In each of the 10 years beginning with 1913, seed from the high-yield plat, the low-yield plat, and the nonpedigreed strain was compared for productiveness. The average yield of each selection for the first and the second 5-year periods of the experiment and the differences between the selections are shown in Table 5. The data show clearly the failure of ear-to-row selection to increase the yield of corn above that which was obtained from mass-selected seed. The efficacy of ear-to-row selection in decreasing productiveness in these experiments is an interesting basis for speculation, but of little importance in the present connection.

TABLE 5.—*The average excess acre yield of the high-yield selection over the nonpedigreed strain and of the high-yield selection and the nonpedigreed strain over the low-yield selection of corn in Illinois*

[Adapted from Smith and Brunson (72, p. 572)]

Designation		Excess of acre yield over—	
		Nonpedigreed strain	Low-yield selection
High-yield selection:			
1913–1917	bushels	1.3	5.8
1918–1922	do	1.5	15.2
Nonpedigreed strain:			
1913–1917	do		4.5
1918–1922	do		13.7

Varieties that have been developed by ear-to-row selection have been included in many varietal comparisons and frequently have ranked at or near the top of the list. There are few if any varietal comparisons which have continued over a series of years, however, in which varieties developed by ear-to-row selection have been significantly more productive than the better of the mass-selected varieties. This failure to produce outstanding varieties constitutes the best evidence of the fallacy of ear-to-row selection as a method of corn improvement.

PLACE OF EAR-TO-ROW SELECTION

It is probable that the yield of an entirely unselected or unadapted variety could be improved by one or two years of careful ear-to-row selection. It is questionable, however, whether the improvement would be enough more than that which could be had by mass selection to warrant the extra trouble and expense of the more elaborate method. Certainly there is nothing in the experimental evidence to show that ear-to-row selection is worth while in a variety that already is well adapted. More rapid progress in altering such characteristics as height of ear, height of plant, chemical composition of the kernel, and the like probably can be made by ear-to-row selection than by mass selection. Such alterations, however, can be achieved so much more rapidly by selection within selfed lines that it is improbable that ear-to-row selection has any real place in present-day corn improvement.

HYBRIDIZATION

Many of our present agronomic varieties of corn originated as intentional or accidental hybrids. Thus, Reid originated from a mixture (with consequent crossing) of Gordon Hopkins corn and an early-maturing yellow variety grown generally in Tazewell County, Ill. The Gordon Hopkins corn, seed of which was brought from Brown County, Ohio, failed to mature well in Illinois in 1846. The immature seed from this crop produced a poor stand when planted in 1847, and the missing hills were replanted with local corn. Seed from the mixed crop of 1847 was the foundation stock from which Reid was developed by careful selection. Many other varieties originated similarly.

This is typical of the usual function of hybridization in plant breeding. Indeed, plant breeding consists essentially in hybridizing to create new combinations from which to obtain the best by selection. Because of the fact that corn is cross-fertilized so largely, even the most carefully selected varieties are only mixtures of hybrids within which there already is an abundance of variation. Hybridization as a basis for obtaining new combinations consequently has not played an important part in recent corn improvement. The present discussion will be limited, therefore, to the utilization of F_1 crosses between varieties of corn as a means of obtaining larger yields.

As early as 1876, Beal (*5*) of the Michigan Agricultural Experiment Station called attention to the larger yields frequently obtained in the first generation after crossing two varieties of corn and suggested that such F_1 generation crosses or hybrids might be used to obtain increased corn yields generally.

Many crosses between varieties of corn have been compared with their parents. The yields of 244 crosses between standard varieties of corn, previously summarized (*62*), may well be taken as an example of what is to be expected in such comparisons. Of the 244 crosses, 201 yielded more than the average of the parents and 43 yielded less than this average. This is striking evidence of the tendency of hybrid vigor to increase yields. It does not mean that all of the 201 were really advantageous crosses, however. Such a cross must yield more than the best local varieties to be worth growing commercially. Of the 244 crosses referred to, 86 (about one-third) yielded over 5 per cent more than the better parent. There is no way of telling exactly how many of them were better than the best local varieties, but possibly less than 25, or about 1 out of every 10.

MAINTAINING HYBRID SEED

As hybrid vigor is limited to the first generation, it is necessary to produce the hybrid seed each year (or a supply for two years every alternate year). A plan has been suggested for doing this conveniently while at the same time maintaining pure seed stocks of the parent varieties (*9*). As this is applicable equally well in producing seed of crosses between selfed lines, it will be given in some detail.

Two varieties, A and B, are grown in alternate rows in a small field sufficiently isolated from other corn to prevent mixing. If variety B is to be the pollen parent the first year, the tassels are pulled from all of the A plants as they appear and before they have shed any pollen. The silks on the A plants then are pollinated by pollen from the B plants, and the ears represent the cross A × B, giving the pistillate (female) parent (A) first. As none of the A plants shed pollen, the ears of B are pure, and seed may be selected from them to maintain this variety. Either of two plans may be followed the second year. If enough hybrid seed for two years was produced the first year, only a small plat of A need be grown in order to maintain a stock of this variety. This plan should be followed unless it is known that the reciprocal crosses of the varieties, in this case A × B and B × A, are equal in productiveness. If they are equal, A and B may be planted in alternate rows again the second year, but this time the B plants are to be detasseled. Seed of the cross B × A and pure seed of A then will be obtained. The work of the third year will be like that of the first year in either event, and seed of both parents and the cross may be obtained conveniently.

The tassels may be pulled easily just when they are emerging from the "boot," as the upper whorl of leaves that incloses the tassel frequently is called. The early morning is the best time for this work, as tassels can be pulled more easily and plants may be detasseled then that otherwise might shed pollen later in the day. During the peak of the tasseling period the crossing plat should be gone over each day, whereas every other day is often enough at the beginning and toward the end of the tasseling period.

PLACE OF VARIETAL HYBRIDS

There are certain specific conditions under which a larger proportion of high-yielding first-generation crosses possibly may be expected than that indicated by the experiments referred to. Crosses between early flint and dent varieties have given promising results for growing under short-season conditions. Similarly, crosses between single-eared and prolific varieties have shown possibilities for use in the southern edge of the Corn Belt. Even so, the crosses must be tested individually over a series of years and on different soils before the profitable ones can be known. Moreover, even if a cross, between Reid and Leaming for example, were shown to be high yielding, this evidence would apply only to the cross between the specific strains that were used as parents. Crosses between other strains of these varieties might produce inferior yields.

Growing F_1 crosses between varieties of corn has possibilities as a means of obtaining increased yields. It also is somewhat complicated and can be utilized only after specific crosses have been shown to be profitable experimentally. The method does not seem to offer the promise that crosses between selfed lines do under most conditions and probably has little place as a method of increasing corn yields. On the other hand, it may be of much importance under special conditions when it is desired to combine in the F_1 hybrid the dominant traits from each of two varieties.

SELECTION WITHIN SELFED LINES

Selection within self-fertilized lines, or selfed lines, as they may be called for brevity, is a principle rather than a method of breeding. It consists essentially in (1) the isolation by self-fertilization and selection of lines that breed true, more or less, for certain characters, (2) the determination of which lines are more productive, and (3) the utilization of such selfed lines commercially in various ways. Selection within selfed lines has developed into the present basis for corn improvement primarily as a result of advances in the science of genetics. Earlier efforts had shown that mass selection and ear-to-row selection were effective in increasing adaptation and yield within limits. It also had been shown that close breeding tended to result in decreased productiveness, whereas cross breeding frequently resulted in larger yields. The theory of Mendelian inheritance, which already has been considered, explained why the progress under mass selection and ear-to-row selection was limited. Of more importance, it suggested a sounder basis for improvement.

The first suggestion for utilizing selection within selfed lines in practical corn breeding was made by Shull in 1908 and 1909 (*68*, *69*), the following being quoted from the summary of his 1909 paper:

> The process [the pure-line method] may be considered under two heads: (1) Finding the best pure lines; and (2) The practical use of the pure lines in the production of seed corn.
>
> (1) In finding the best pure lines it will be necessary to make as many self-fertilizations as practicable and to continue these year after year until the homozygous state is nearly or quite attained. Then all possible crosses are to be made among these different pure strains and the F_1 plants coming from each such cross are to be grown in the form of an ear-to-the-row test, each row being the product of a different cross. These cross-bred rows are then studied as to yield and the possession of other desirable qualities. One combination will be best suited for one purpose, another for another purpose. Thus, if the self-fertilized strains be designated by the letters of the alphabet, it may be found that the cross C×H will give 120 bushels per acre of high-protein corn, that F×L produces a similar yield of low-protein corn, that K×C gives the highest oil-content accompanied by high yield, and so on. Moreover, it seems not improbable that different combinations may be found to give the best results in different localities and on different types of soils. The exchange of pure-bred strains among the various experiment stations greatly increases the number of different possible hybrid combinations and facilitates the finding of the best combination for each locality and condition.
>
> (2) After having found the right pair of pure strains for the attainment of any desired result in the way of yield and quality, the method of producing seed corn for the general crop is a very simple though somewhat costly process. (*69*, *p. 57–58.*)

The poor quality and the high cost of the seed produced on the weak plants of the earlier selfed lines were obstacles to the practical utilization of the method. In spite of this, experiments on selection within selfed lines were undertaken by a number of investigators. The use of double crosses, or crosses between crosses, suggested by Jones (*39*) did much to obviate the objections. A little later Hayes and Garber (*27*) emphasized the possibility of utilizing synthetic varieties. Both of these suggestions apply to the utilization of selfed lines and will be considered in that connection. Reference should be made here, however, to the effect that the change in concept of the cause of hybrid vigor had on the theory of breeding by selection within selfed lines.

At the time that Shull's suggestion was made for using selfed lines in corn breeding, it was thought that hybrid vigor was a phenomenon of physiologic stimulation. Under such a hypothesis selfed lines could be used only as a basis for obtaining hybrid combinations of one kind or another. The Mendelian interpretation of hybrid vigor as due to the complementary action of favorable dominant factors, which already has been discussed (p. 22), was not suggested until 1910 (*7*, *44*). It was not generally accepted until after Jones (*38*) had shown in 1917 that the existence of linkage overcame certain theoretical objections that had been raised. More recently Collins (*12*) has demonstrated that these objections were invalid in any event.

Under this interpretation of hybrid vigor it should be possible to obtain high-yielding selfed lines for direct utilization. These could be obtained either by extensive selection or by systematically building up better lines by selection with alternate periods of selfing and cross-fertilization. Thus, a productive F_1 hybrid could be mated back to its better inbred parent for several generations, selecting seed only from the most vigorous plants each year. In this way a strain could be produced that would be homozygous for most of the favorable factors of the better parent and heterozygous for at least many of the favorable dominant factors of the other parent. Selection in such a strain should produce much better selfed lines than those now available.

Although there is no direct evidence as yet, there is some indirect evidence, as well as good theoretical reason, for believing that high-yielding selfed lines can be obtained. If so, their utilization will be simple and needs no specific consideration. Selection within selfed lines will be discussed here, therefore, primarily from the standpoint of obtaining lines for use in hybrid combination.

In practice, a number of desirable plants are self-pollinated. The seed from the better plants is planted an ear to a row. Self-pollinations then are made among the progeny plants, from among which selection is continued in the same way. After the various lines begin to breed relatively true, crosses are made between them and compared for productiveness. The lines that produce the higher yielding and more desirable crosses then may be combined into single or double crosses or into synthetic varieties for commercial utilization. The better crosses also may be used as a basis for further selection in attempts to build up more desirable selfed lines.

No definite rules can be given for the number of lines to be carried, pollinations to be made, or crosses to be compared. The question is one of selection, and the larger the quantity of material from which to select the better are the chances of success. An outline showing the pedigrees of the different lines of a family from a single open-pollinated kernel through a 6-year period is shown in Figure 7. This will give an idea of the way that selection may be practiced within a single family in different years.

The corn-breeding program being carried cooperatively by the Office of Cereal Crops and Diseases of the Bureau of Plant Industry and the Iowa Agricultural Experiment Station may be used to show the numbers involved in a comprehensive breeding program. From 2,000 to 3,000 ear rows have been grown each year in this experiment from selfed seed tracing back to 500 original open-fertilized ears

of 16 standard Iowa varieties of corn. From 7,000 to 12,000 self-pollinations have been made each year as a basis for selection, and

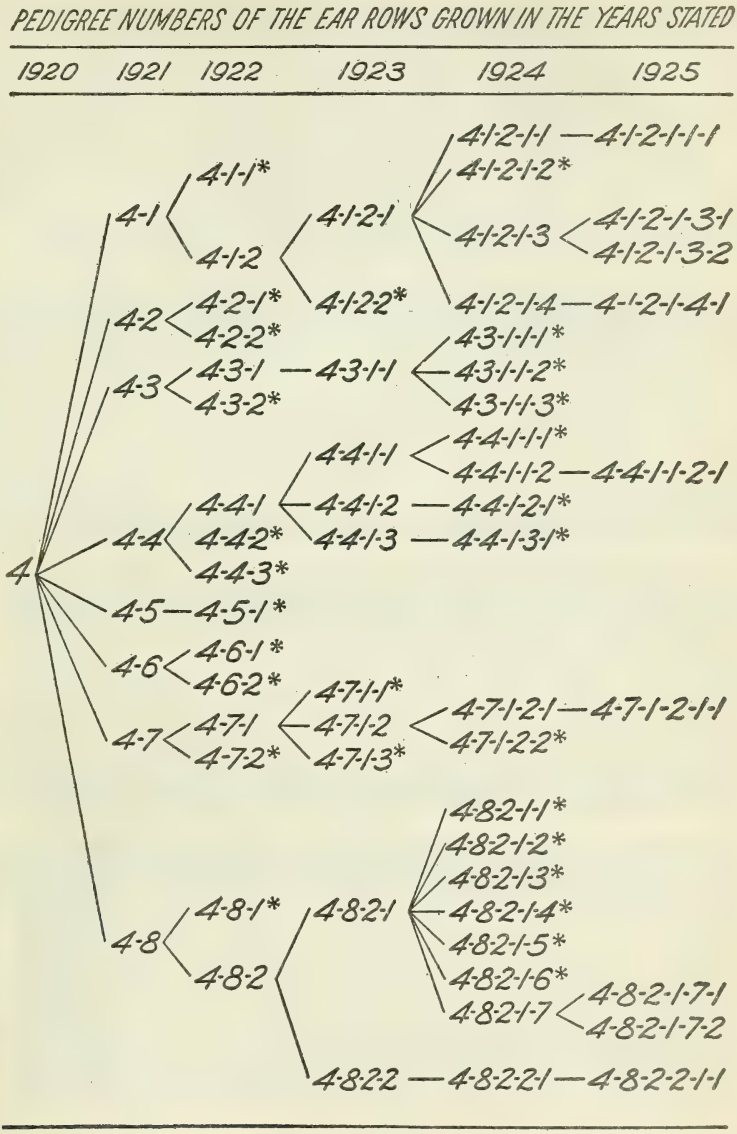


FIG. 7.—Outline of the pedigrees within a single family (No. 4) of selfed lines during six generations. The pedigree numbers are of the ear rows grown from selfed ears in the years stated. Each ear row from which no seed was selected for continuing the lines is marked with an asterisk

more than 3,000 cross-pollinated ears, representing 480 combinations between 80 unrelated lines, were obtained for use in the first comparison of crosses.

HAND POLLINATING

In order to control pollination definitely, whether in selfing or crossing, it is necessary to pollinate by hand. Briefly, hand pollinating consists (1) in protecting the silks from any pollen until enough silks have emerged; (2) in collecting and applying uncontaminated pollen from the selected plant; and (3) in again protecting the silks from any stray or foreign pollen. Paper bags are used for protecting the silks before and after pollinating and for collecting the pollen that is used. This operation is relatively simple, although the large numbers of pollinations that must be made require much time and attention in the aggregate.

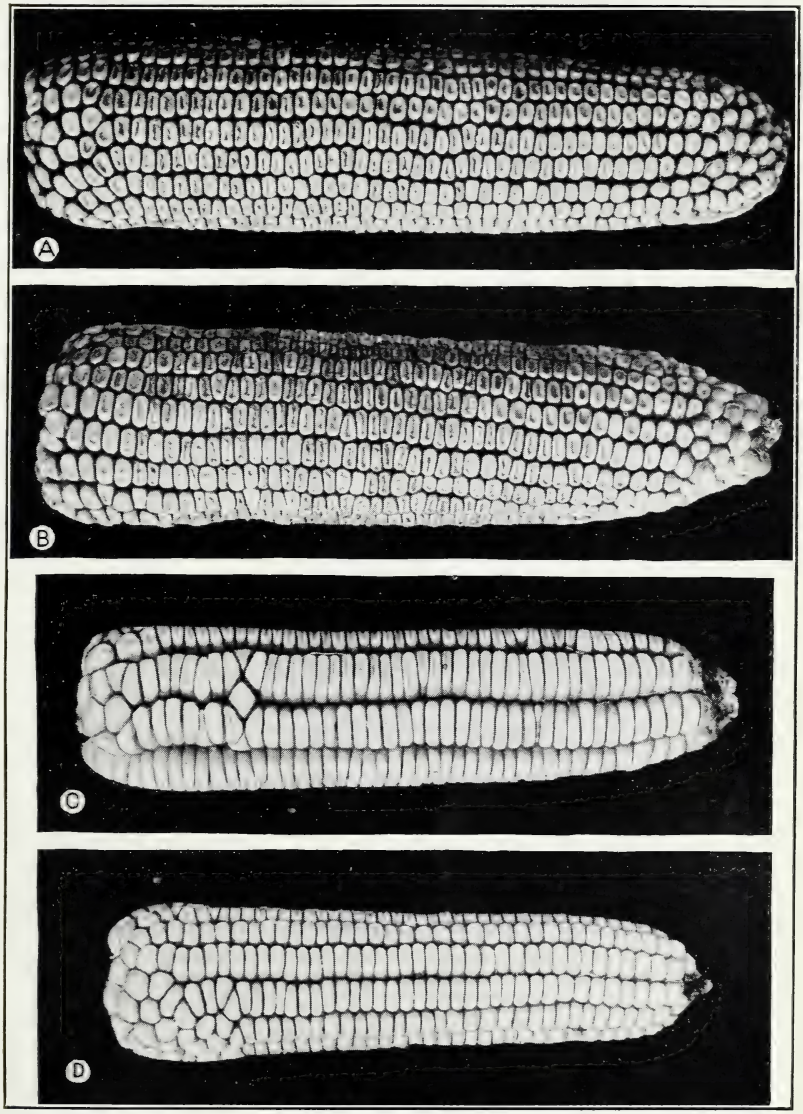
Normally, most corn plants begin to shed pollen a day or more before their silks appear. The ear shoots usually emerge from between the leaf sheath and culm at one or more nodes at about the time of tasseling (pl. 9), and two or more days elapse in general between the first appearance of the ear shoot and the emergence of the earliest silks from the enveloping husks.

Pollen usually is shed first from the anthers toward the tip of the central spike of the tassel (pl. 2, A). Shedding then proceeds downward along the central and lateral spikes. The same tassel may continue to shed pollen for a week or more, although there is much variation in the duration of shedding, depending upon the strain of corn and the condition of the weather. Pollen is shed most abundantly during the two or three hours in the morning after the dew has dried off. Shedding continues during the day, however, and there may be secondary peaks of more active shedding following showers or even after periods of cloudiness.

There is some question as to the length of time pollen will remain viable. Practically, it is safe to assume that pollen will not be viable on the day after it was shed. Contact with moisture will cause pollen to burst and lose its viability. After some experience, poor pollen usually can be distinguished from good by the way it looks when poured from the bag.

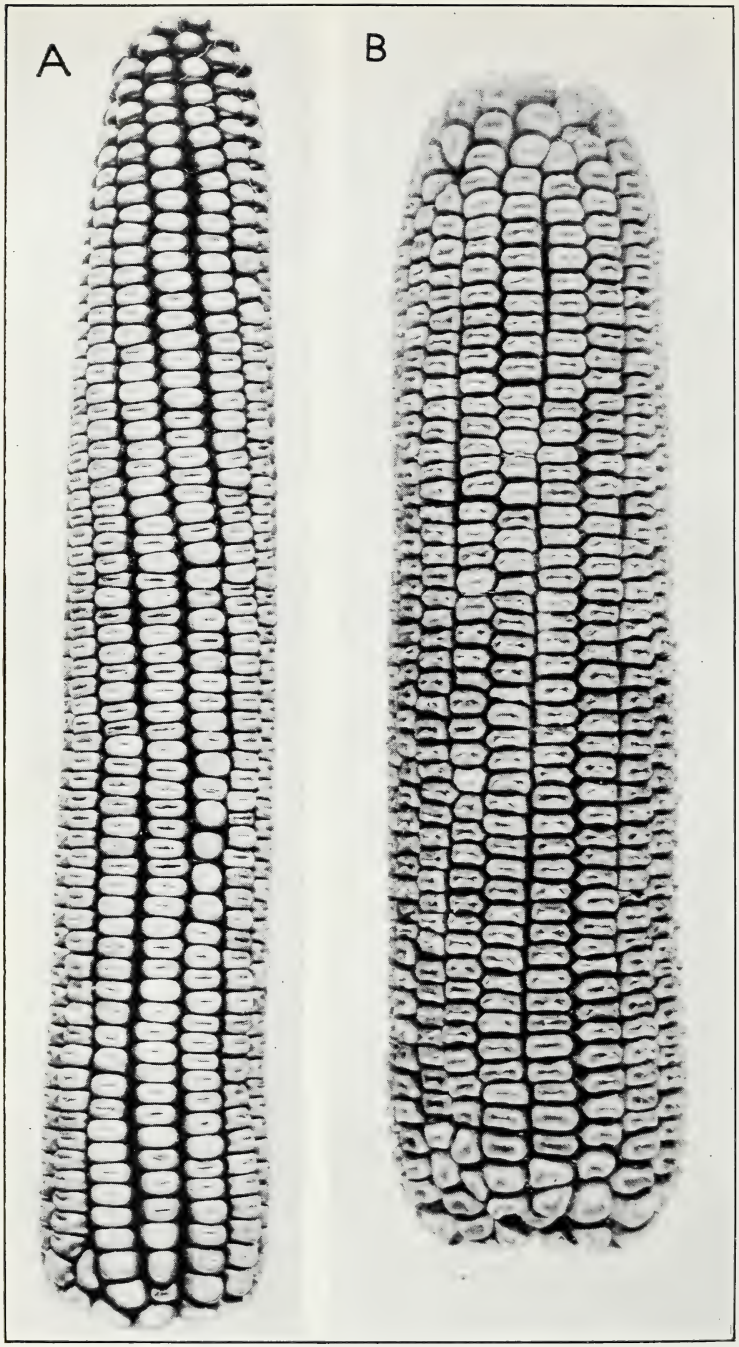
There are many exceptions to these general conditions. In some strains the silks will emerge from the ear shoots before the latter appear. Other strains will silk before shedding pollen. Moreover, the entire blossoming process is affected markedly by the climatic conditions. Not only may the rate of the process be modified, but the entire order may be reversed. The best ways to meet the various unusual conditions that occur during hand pollinating are details that can be learned only by experience. The present description is limited to what occurs normally under the conditions in most parts of the United States.

Although any well-made bag of suitable size may be used for bagging the ear shoots before pollination, small bags made of a heavy glassine or a vegetable parchment paper are more convenient. These are transparent enough so that the emergence of the silks may be seen without removing the bag, saving time and eliminating one chance of contamination with stray pollen. Many corn breeders are using a bag 2½ by 6 inches made of triple-strength glassine paper with a safety folded bottom and glued with waterproof glue. Others prefer a larger bag made of parchment. Whatever the size, the



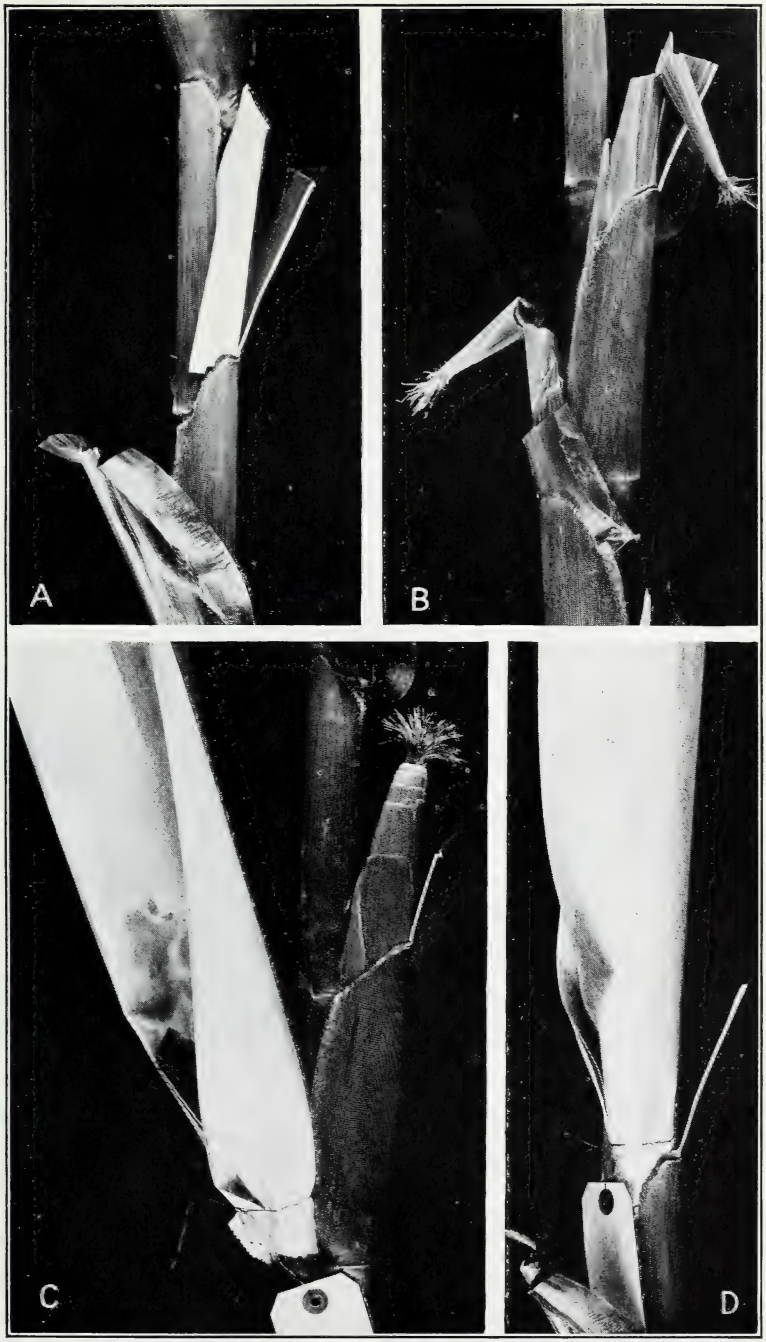
VARIETIES OF CORN, SHOWING DIFFERENCES IN THE IDEALS OF THE BREEDERS WHO SELECTED THEM

A, Reid; B, Leaming; C, Hickory King; D, Marlboro Prolific



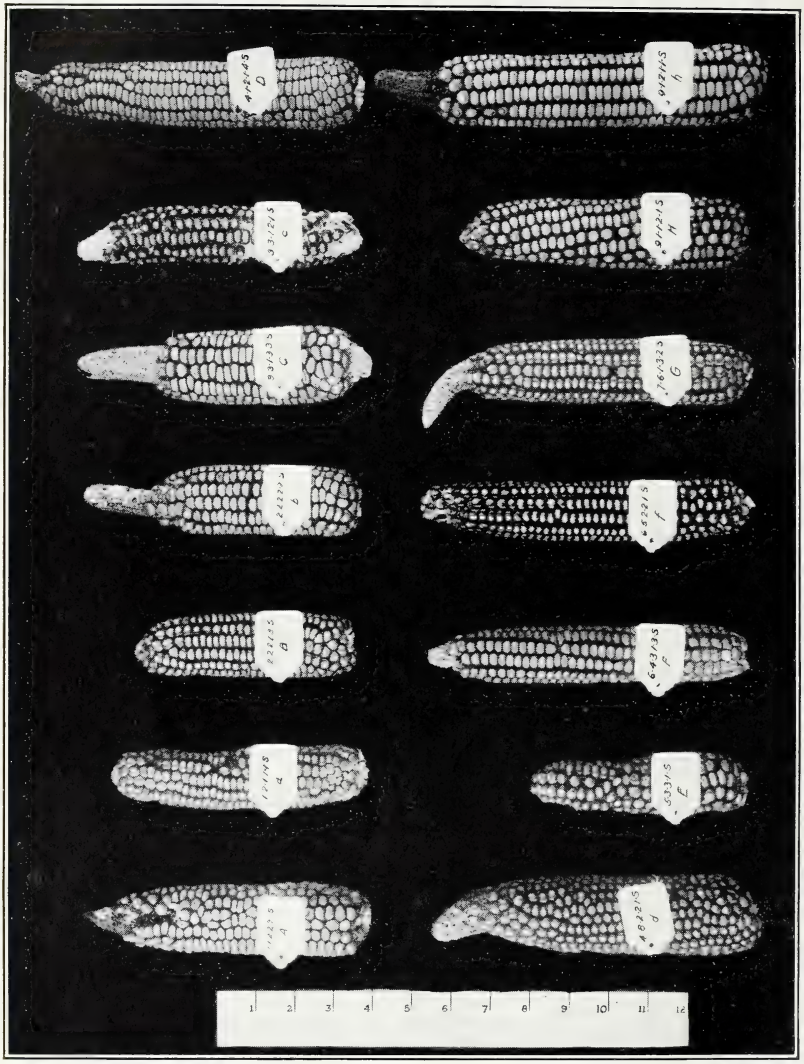
TWO CONTRASTED EARS OF CORN

Longer ears with fewer rows of smoother heavier kernels (A) have been slightly more productive in a number of experiments than the rougher ears of the old "show type" (B)



METHODS OF HAND POLLINATING

A, Shoot bagged before pollination
B, Shoots cut back after first silks emerged, having been bagged before the silks appeared and to be rebagged as in A, C, and D. Two methods of bagging shoots after pollinating are shown
C, Shoot with a desirable brush of silks ready to pollinate 24 hours after being cut back as in B



BREEDING EARS OF 14 SELFED LINES OF C. I. No. 228 CORN PLANTED IN 1926

The pedigree number of each ear and a temporary index letter used for convenience are on the tags. These letters are used to designate the plants of the different lines and crosses illustrated in Plates 11 and 12

REPRESENTATIVE PLANTS OF THE SELFED LINES OF C. I. NO. 228 CORN AND OF CROSSES BETWEEN LINES

The index letters are the same as those shown in Plate 10. A plant of the Lancaster Surecrop variety (O. F.) is shown for comparison

REPRESENTATIVE PLANTS OF THE SELFED LINES OF C. I. NO. 228 CORN AND OF CROSSES BETWEEN LINES

The index letters are the same as those shown in Plate 10. A plant of the Lancaster Surecrop variety (O. F.) is shown for comparison

bags should be well made. Nothing is more distressing than to go to the field after a storm and find the work of days lost because bags have become unglued, torn, or blown off. The larger bags may be fastened to the ear shoot, culm, or both, with string, wire, or a paper clip. The smaller bags may be slipped over the ear shoot and between it and the culm, utilizing the natural pressure between the ear shoot and culm to hold them in place (pl. 9, A). The latter practice may be followed after some experience, with negligible losses due to the bags blowing off.

The tassel bags, used for collecting pollen and later for protecting the pollinated shoot or ear, must be larger (pl. 9, C and D). Square-bottom bags made of good manila or hemp stock have proved very satisfactory for tassel bags. These may be fastened around the stem of the tassel with string, wire, or a paper clip. Bags of the 12-pound size are convenient for large varieties of corn, and 10-pound, 8-pound, or even 4-pound bags are better for some of the smaller sorts.

As the plants begin to tassel the plat is visited each day and ear shoots on desirable plants are bagged before their silks have emerged. Nothing more is necessary until the first silks of the bagged ear shoots appear. Other things being equal, the number of kernels obtained will depend upon the number of silks pollinated. Consequently, it is better not to pollinate until most of the silks have emerged. The silks are receptive even before they emerge from the enveloping husks and usually remain receptive for several days afterwards. Pollination should not be delayed longer than necessary, however, both because some of the silks may have become unreceptive and because too large a mass of silks interferes with pollination and promotes the development of molds after the pollinated shoot is rebagged. It has been found convenient and efficient to cut off from one-half to 2 inches of the ear shoot after the first silks have emerged (pl. 9, B). A shoot cut back one day usually will present an even brush of silks ready to pollinate on the next (pl. 9, C), although occasionally this is not the case.

Pollen should be used only from tassels that have been bagged since the preceding day. This insures that any stray pollen which may have lodged on the tassel prior to bagging will have lost its viability. When self-pollinating, if the tassel is bagged at the time the ear shoot is cut back the bagged tassels mark the plants that will be ready to pollinate the next day. This is a convenience and permits these plants to be handled immediately in case of a threatened shower which would wet the tassel bags and delay pollination until they had dried again and fresh pollen had been shed.

Every care should be taken to prevent contamination from stray pollen. The air is filled with pollen at pollinating time, and the corn leaves and the hands and clothing of the operator carry liberal quantities. The silks should be exposed as little as possible, and should not be allowed to come in contact with anything that may carry pollen. Tearing off the end of the shoot bag and applying the pollen through the opening reduces the chances for contamination. Another practice is to fold the tassel bag so that the pollen will not pour out, and to cover the shoot with the open part of the tassel bag before removing the bag protecting the shoot. The tassel bag then may be straightened up quickly so that the pollen will fall on the

silks within it. One of the best aids in preventing stray pollination is to apply an abundance of pollen of the desired kind. Very little pollen is needed to pollinate all of the silks on a shoot. Using plenty, however, reduces the likelihood of stray pollen grains functioning even if they reach the silks.

Another method of controlled pollination that has been found highly efficient under some conditions has been described (*36*). With this method the shedding tassel is cut off and bagged with the ear shoot at the time the latter is cut back. The stem of the tassel is inserted in a small bottle of water attached to the stalk below the ear. Under favorable conditions the tassel will continue to shed pollen for two or three days, the silks thus being pollinated as they emerge.

SELECTION

Selection is just as essential when working with selfed lines as in open-fertilized material. Indeed, it is more essential. The purpose of selfing is to fix what is selected. Fixation is relatively slow and may never be accomplished in open-fertilized corn. Characters become fixed relatively soon under self-fertilization and then are no longer modified. It obviously is important, therefore, that many of the unfavorable characters be eliminated as quickly as possible. Selection should begin with the plants furnishing the foundation stock and should be continued at each step where there is opportunity. This means that only the best kernels on the ears from the best plants in the best individual rows of one season should be used for the next season's breeding stock.

Selection for general kernel type should be practiced among the ears rather than among the kernels of the individual ears. The most careful selection among the kernels is warranted, however, when kernel characters such as endosperm texture, composition, or color are involved. Thus, selecting the white kernels from a selfed ear segregating for kernels with yellow and white endosperms will fix this character immediately. Selection of the deepest yellow kernels, on the other hand, will increase materially the proportion of homozygous yellow ears in the progeny. Defective kernels already have been illustrated (pl. 5, C and D) and discussed briefly in connection with heritable characters. Some kernels are so defective that they would be eliminated by failing to germinate even if planted. Other defects are not so marked, and, if not eliminated by conscious selection, may become fixed as undesirable characters in otherwise excellent lines.

Plant selection among and within selfed lines may be considered for convenience from two points of view, (1) eliminating the worst and (2) retaining the best. The first condition that confronts the breeder working with selfed lines of corn is the large number of abnormal plant types that occur. Albino, virescent, and pale-green seedlings are noted, as well as seedlings that are malformed in one way or another. Thus, in one breeding experiment, of the 2,750 progenies from ears self-fertilized for the first time, 532 (14 per cent) segregated for some form of seedling chlorophyll abnormality (*37*). In another experiment 1,872 progenies were grown from seed selfed for the first time and representing 468 different stocks of

corn. Of these, 681 (36 per cent) segregated for different seedling abnormalities, the most common being some form of chlorophyll deficiency (*34*). As the plants grow older, other defects become evident. Some chlorophyll deficiencies do not develop until after the seedling stage. Aberrant conditions of the inflorescences, including complete sterility of the staminate or pistillate parts, appear at blossoming time, and there may be evidences of an unbalanced metabolism such as striping or firing of the leaves. All of these conditions—and only a few examples have been mentioned—are undesirable from the standpoint of corn production and are to be eliminated from the breeding stocks. Furthermore, although many of them would be eliminated automatically sooner or later, it is important to weed them out promptly. Their presence tends to result in grossly irregular stands of uneven plants and so obscures the less striking differences that occur. It is good practice to increase temporarily the number of lines representing a strain that is segregating for some striking abnormality so as to permit eliminating the abnormality as quickly as possible if it is desired to maintain the strain.

So much for the elimination of the grossly unfit, or what may be called negative selection. The decision as to what direction positive selection shall take is more difficult. Selection for productiveness among the plants and ears will be on much the same basis as in mass selection in open-fertilized corn, namely, the production of sound grain from normal plants. The exact type of ear and plant will differ with the locality for which the corn is being selected. The evidence from experiments with open-fertilized corn that relatively long ears with not too many rows of moderately wide, thick kernels tend to be more productive suggests this type as desirable also in selfed lines. In fact, there already is some evidence that an association exists between this type of ear and productive selfed lines (*30*, *52*). It seems probable that too much attention to type of ear is not warranted in selecting within selfed lines any more than in open-fertilized corn. When opportunity presents to select between ears from equally desirable plants, however, the longer ears with larger kernels probably should be chosen. Where some plant character such as height of plant, height of ear, freedom from suckers, husk protection against insect attack, or the like is the improvement sought, it obviously will be the basis of selection. Otherwise, about all that can be done is to select from the more productive plants that are of a type and length of season adapted to the conditions where the corn is to be grown and as free as possible from disease. The final selection is to be based upon the measured yield of the lines in hybrid combination, and up to the present no characters have been found that can be used to tell which selfed lines will produce the highest yielding crosses.

It is obvious that the foregoing consideration of plant selection as an elimination of the worst and a retention of the best is a matter of convenience only. Clearly, the dividing line is arbitrary. At the same time, this difference occurs naturally in the actual practice of selection. Most of the selection in the earlier stages of the breeding program of necessity consists in discarding the grossly unfit. So many abnormal characters occur that less obvious differences are

masked. As the program advances, the stocks segregate for fewer striking characters and opportunity is presented to select the better functioning (or to eliminate the less efficient) lines. Finally, the selected lines are crossed and the crosses of one kind or another are compared to afford a basis for the final selection of those selfed lines which produce the best hybrid combination.

An idea of the opportunity for selection that exists in the later phases of the breeding program may be had from Plates 10, 11, and 12, which illustrate representative ears and plants of Cereal Investigations (C. I.) No. 228. This number was given a single open-pollinated ear of the Lancaster Surecrop variety of corn. Nine plants from kernels on this ear were self-pollinated in 1920. The resulting ears were the parent stocks for nine families of selfed lines, one of which (No. 8) was discarded. The pedigree numbers of family No. 4 are shown in Figure 7. The breeding ears for 14 lines from these 8 families planted in 1926 are shown in Plate 10. Representative plants of some of the lines and of crosses between them are shown in Plates 11 and 12. That the opportunity for selection is not limited to the selfed lines is shown clearly by the variation that exists among the crosses. The plants in Plate 11 have been arranged to show particularly the uniformity with which some lines may influence their crosses. The plants in Plate 12 are arranged to show primarily the relative size of the parent lines and their crosses in comparison with a representative open-fertilized (O. F.) plant of the Lancaster variety.

Positive selection for relatively simple characteristics may be practiced in the selfed lines with reasonable assurance that if lines breeding true are obtained some of the crosses between these lines also will exhibit the desired characteristic. Because of the importance of this concept it is desirable to illustrate it with a hypothetical case. This may be used also as an example of why selection within selfed lines is so much more efficient than mass selection in modifying qualitative characters.

Aleurone color, the mode of inheritance of which already has been described (p. 11), affords a convenient example. Assume that a variety of corn is homozygous for the factors *A A*, *Pr Pr*, and *i i*, and heterozygous for the factors *C c* and *R r*. As all of the plants are alike for the first three factor pairs, they need not be considered further, the aleurone color of the kernels being determined by the factors *C c* and *R r*. The following nine classes of kernels would be produced in such a variety:

Purple aleurone: (1) ***C C R R***, (2) ***C C R r***, (3) ***C c R R***, (4) ***C c R r***.
Colorless aleurone: (5) ***C C r r***, (6) ***C c r r***, (7) ***c c r r***, (8) ***c c R r***, (9) ***c c R R***.

Consider now the results of specific selection for purple aleurone, colorless aleurone being assumed undesirable. Purple kernels from each of a number of ears would be planted an ear to a row, and some of the resulting plants in each row would be self-pollinated. Three classes of ears would be obtained: (a) Ears with all kernels purple, from seed of class 1; (b) ears having three kernels with purple to 1 kernel with colorless aleurone, from seed of classes 2 and 3; and (c) ears having 9 kernels with purple aleurone to 7 with colorless aleurone, from seed of class 4. The seed on each ear having all kernels

purple would produce only plants having ears with purple kernels, regardless of how these plants were crossed among themselves.

If the object were to eliminate kernels with purple aleurone, the problem would be more difficult. Seed of each of the classes 5 to 9 would breed true for colorless aleurone as long as the plants were self-pollinated or as long as no cross occurred bringing *C* and *R* together. Crosses of either 5 or 6 on the one hand, with 8 or 9 on the other, would have all or some purple seeds. The lines that could be crossed without producing purple kernels could be determined only by experiment. Once determined, however, the selected lines could be combined into an F_1 cross year after year, with the knowledge that the cross would produce only nonpurple kernels.

This illustrates well the difference between the certainty of success of selection within selfed lines in obtaining the desired condition for such a relatively simple character and the almost equal certainty of failure of selection in open-fertilized corn. Under selection within selfed lines the production of a variety of corn with purple or white kernels can be undertaken with the definite knowledge that it will be obtained. Under selection in open-fertilized material the only hope of obtaining a purple sort would lie in the chance of planting nothing but kernels of class 1 in some season. That this is a chance is evident from the fact that the kernels in class 1 are indistinguishable practically from those in classes 2, 3, and 4. Success of selection for a variety with colorless aleurone in open-fertilized corn would equally be dependent upon chance. Only the accidental selection of all seed ears either in one or more of classes 5, 6, and 7, or in one or more of classes 7, 8, and 9, would insure against purple seeds in later generations.

Except as the possibilities for obtaining specific characters were considered, the preceding discussion of selection has been from the point of view of obtaining desirable selfed lines. It obviously is necessary to have reasonably productive lines because of the practical considerations of seed production. How effective selection will be during the earlier generations is not certain. Some data show little relation between the characters of lines in the first and in the fifth generations (*42*). Other data show a definite tendency for lines to behave similarly in successive generations both with regard to yield (*30*, *64*) and with regard to other characters studied (*30*). The effectiveness of selection in the earlier generations presumably would differ in different varieties. Close-bred strains should become fixed more quickly, whereas more heterozygous stocks would respond less quickly.

Whether the more productive selfed lines will produce the higher yielding crosses is even less certain, some data indicating that they do (*48*) and other data showing no general relation (*64*). It is easy to see why such a relation should be obscure, or possibly not exist. Consider, for example, a line breeding true for dwarfness, owing to a simple recessive factor. Such a line might carry also an unusually desirable complement of dominant favorable factors which, nevertheless, could not produce large plants or yields because of the dwarfing action of the single pair of factors. The expression of all the favorable dominant factors carried by the dwarf line would be permitted in crosses between it and any other lines carrying the

allelomorph dominant to dwarfness. Such crosses consequently would be unusually vigorous and productive and would tend to indicate a negative relation between the yields of the parents and the crosses.

It is not improbable that lines homozygous for very deleterious characters frequently may carry a superior assortment of other factors. It has been shown that a stock segregating for dwarf plants produced a marked deficiency of dwarfs under field conditions and a smaller deficiency in the greenhouse where conditions for emergence were more favorable (*23*, *45*). This may mean that many of the plants surviving in the field were those with the better assortments of other factors. That is, dwarfness or other deleterious characters may tend to eliminate individuals with the less desirable complements of general growth factors by increasing the difficulty of survival. If such a condition exists it might even be utilized as a means of selection were it not for the practical necessity for producing a good quality of seed at reasonably low cost.

UTILIZATION OF SELFED LINES

The first suggestion of selection within selfed lines as a method of corn breeding resulted from investigations planned primarily to study various genetic principles. In spite of the inferiority of the selfed lines obtained, it was noted that the crosses between these lines were vigorous and that some yielded more than the original variety. As a consequence it was suggested that such crosses could be utilized commercially (*69*). The greatest objections to this were (1) that the selfed lines were unproductive, making the cost of the seed high, and (2) that the seed produced on the selfed plants was of poor quality so that it might not germinate well under unfavorable conditions. It then was suggested that crosses between crosses, or double crosses, as they were called, be used commercially (*39*, *40*). For example, letting A, B, C, and D designate four unrelated selfed lines, crosses would be made between A and B and between C and D. These two single crosses then would be crossed and the first generation of the seed from the resulting double cross, (A × B) × (C × D), would be utilized commercially. As double-crossed seed would be produced on vigorous hybrid plants, its production would be cheaper and its quality better. The method of crossing is the same as that already considered under varietal hybridization (p. 33). The system for maintaining a supply of pure seed of the four selfed lines and producing single and double crosses is indicated diagrammatically in Figure 8.

The results of later experiments under more intensive selection indicate that the objections which double crosses were suggested to meet no longer exist. Some of the selfed lines now being obtained are productive enough so that their use in single crosses for commercial seed production will be entirely practical. The idea long has been prevalent, however, that a mixture of seed of two varieties of slightly unlike season would be more productive than the average of the two varieties as grown separately. The theory is that the variation in blossoming and earing would cause the plants of the two varieties to make their maximum demands on the soil at different

times. An extension of this idea to single and double crosses has suggested another possible advantage for the double cross. The plants of a single cross between long-time selfed lines are exceedingly uniform in time of blossoming and earing as well as in other ways. The plants of a double cross are less uniform. Any advantage that such variation might possess, therefore, would be favorable to the double crosses.

So far there have been no critical comparisons between single and double crosses the parent lines of which have all been reasonably productive. The question as to which kind of crosses will yield more, therefore, is unsettled. Furthermore, the question probably will

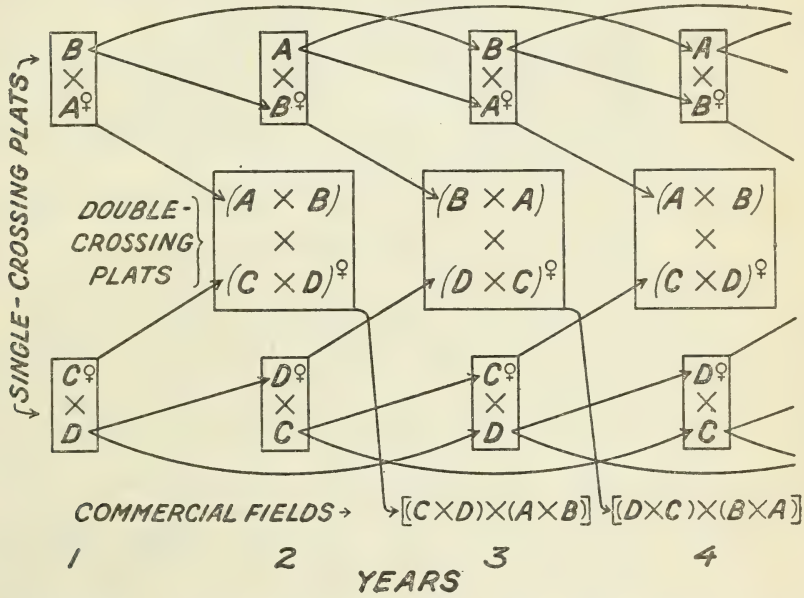


FIG. 8.—Diagram showing the method of producing single and double crossed seed corn. Seed of the single crosses A × B and C × D is obtained the first year from the two isolated single-crossing plats in which the A and the C plants are detasseled. Pure seed of B and of D also is obtained from these plats for use in the second and third years' single-crossing plats. The single crosses obtained the first year are combined into the double cross (C × D) × (A × B) during the second year, the double-crossed seed being used for commercial planting the third year. No seed is saved from the commercial fields. By alternating the direction in which the single crosses are made each year, supplies of pure seed of all four lines may be maintained. The production of single-crossed seed requires the maintenance of only one single-crossing plat each year

remain an open one for some time. The method to be used will be based on questions of economy, practicability, and the like. Both methods have the disadvantage that crossed seed must be produced anew for each season's planting by methods similar to those described under the discussion of varietal hybrids. Double crossing requires that three separate crosses rather than one must be made each year. Unless the double cross has outstanding advantages, therefore, it would seem that the single cross is more likely to find favor.

The use of what have been called synthetic varieties (*27*) was suggested to obviate the necessity of using F_1 crosses each year. A synthetic variety is one created by intercrossing enough selfed lines

so that a degree of hybridity will be maintained by random pollination sufficient to insure productiveness. The ordinary commercial variety of corn in reality is a mixture of crosses or hybrids. Many of the better component elements of these crosses are isolated during the period of selection and self-fertilization. After the value of the selfed lines has been determined in hybrid combination, those lines can be selected which give productive crosses in all combinations. A synthetic variety consisting of a mixture of crosses among these lines grown under conditions of random pollination, as in ordinary corn culture, will be maintained in a high degree of hybridity and at the same time should yield more than the ordinary variety. Theoretically it should be possible to obtain material increases in yield from such synthetic varieties. Theoretically also, such varieties should not be as productive as the F_1 generation of the best component cross. Very little actual evidence is available as yet as to the possibilities of this method. The synthetic variety possesses such practical advantages in the way of seed production that it might well have an important place in corn culture, even though the yields obtained were somewhat less than those from single or double crosses.

The elimination or the fixation of a single characteristic or condition sometimes may be of much importance. Susceptibility to a disease, the development of husks which afford insufficient protection against insect attack, or a tendency to tiller profusely may be a serious disadvantage from the standpoint of the quantity or quality of the crop or of its handling. If the undesirable condition is relatively simple genetically, and particularly if it is due to recessive factors, application of the principles involved in the production of synthetic varieties offers much of value. It was, in fact, in connection with such a problem, the production of a high-oil corn, that the use of this principle first was suggested (*21*). Thus, a large number of unrelated lines may be selected, all of which breed true for the desirable condition of the one character to be modified. These lines then are intercrossed and the mixture of crosses propagated as an ordinary variety under conditions of random pollination. By using enough lines and selecting only for the one character, the recombined lines will differ little, if any, from the original variety except with respect to that one character. The yield or quality will be improved, however, in so far as the character modified previously had been unfavorable.

The operation of this method and the reason that it is particularly applicable in eliminating recessive characters (or in fixing dominant characters) is well illustrated in the hypothetical example of selection for purple and nonpurple aleurone already given (p. 42). Thus, if one selfed ear with all kernels purple were obtained from each of a considerable number of lines, these ears could be shelled together. The mixed seed propagated as a variety would produce only purple kernels. If enough unrelated all-purple ears were not obtained the first season, pollination of plants from purple seeds could be practiced another year, or until enough different lines were represented. The resulting purple variety should be essentially like the parent variety, except for kernel color, but would have any advantages that came from purple kernels.

The production of a synthetic variety with nonpurple aleurone, the recessive condition, would be more difficult. Before combining the lines having nonpurple kernels it would be necessary to determine experimentally that they did not produce purple kernels in any combination. Once determined, however, the proper lines could be combined into a synthetic variety which would breed true for colorless aleurone. If enough independent lines were combined the resulting variety would be approximately the same as the parent variety except for the absence of kernels with purple aleurone.

A relatively simple and unimportant character has been chosen for an example. The basic principles apply equally to any character, no matter how complex, provided its mode of inheritance is known. It is this certainty of selection within selfed lines that makes it so important in corn breeding. Even in the absence of any direct evidence of increased yields following selection within selfed lines, the certainty with which characters can be controlled by this method is sufficient warrant for its use. Fortunately, however, more direct evidence of the success of selection within selfed lines is accumulating rapidly. Some of this evidence will be considered in the paragraphs that follow.

RESULTS OF SELECTION WITHIN SELFED LINES

Most of the data so far available on the results of selection within selfed lines are on the yields of the selfed lines themselves or on crosses or double crosses between lines. The yields obtained from the selfed lines are of little interest. It is enough to say that practically all have been markedly inferior to the parent variety and that no selfed line has been reported which represented an improvement over the parent variety. The proportion of superior lines would be expected to be very small, however, so that the failure to obtain any up to the present is of little importance. The later experiments are encouraging in that much better selfed lines are being obtained under the more extensive selection now being practiced.

It is recognized that not all crosses will be superior, and that the problem of the corn breeder using this method is to find the few which are best. From this point of view the yields of inferior crosses are of as little interest as those of selfed lines and will receive scant attention here. It seems desirable to point out, nevertheless, that some cross has been more productive than the parent variety in every reported experiment in which a number of crosses between selfed lines have been compared.

The first reported yields of crosses between selfed lines in comparison with a comparable noninbred stock appear to be those presented by Shull in 1908 (*68*). The acre yields of reciprocal crosses were 74.4 and 78.6 bushels in comparison with 75 bushels from the parent varieties. In 1909, Shull obtained acre yields of 98.4 and 96.1 bushels from the reciprocal crosses of the best hybrid combination and only 88.1 bushels from the best noninbred strain (*69*). In 1910, 7 crosses averaged 68.07 bushels per acre as compared with an average yield of 61.52 bushels from 10 noninbred strains (*70*). It was on the basis of the experiments in connection with which these yields were ob-

tained that Shull recommended selection within selfed lines as a method of corn breeding.

The data reported by Shull are chiefly of historical interest from the standpoint of the present discussion. In a similar category are the experiments with crosses at the Connecticut station begun by East and reported in detail by East and Hayes (*19*). The latter have the added interest that some of the lines started by East and continued by Hayes and finally by Jones are the parents of the double cross known to all corn breeders as Burr-Leaming. Burr-Leaming is a cross of two selfed lines of the Burr variety crossed with a cross between two selfed lines of the Leaming variety. The productiveness of this double cross under many of the conditions under which it has been tested has done more, perhaps, than any other single factor to arouse interest in selection within selfed lines as a basis for corn improvement. The comparative yields of Burr-Leaming and five of the highest yielding commercial varieties grown at Mount Carmel, Conn., during the 5-year period 1918 to 1922, as reported by Jones and Mangelsdorf (*43*), are given in Table 6.

TABLE 6.—*Comparative acre yields of shelled corn of the double cross, Burr-Leaming, and of five high-yielding varieties at Mount Carmel, Conn., 1918–1922*

[Data from Jones and Mangelsdorf (*43, p. 161*). The highest yielding of the commercial varieties in each year is marked with an asterisk (*)]

Designation of variety	Acre yields of shelled corn (bushels)					
	1918	1919	1920	1921	1922	Average
Burr-Leaming (double cross)	116	88	55	95	63	83.4
Beardsley's Leaming	*96	54	51	85	48	66.8
Luce's Favorite	-------	*79	38	81	50	62.0
Webber	81	62	*57	73	49	64.4
Northern White	84	75	32	*87	-------	69.5
Century	68	51	55	77	*67	63.6
Average of five varieties	[1] 82.3	64.2	46.6	80.6	[1] 53.5	65.4

[1] Average of four varieties only.

The data on the varieties are typical of varietal experiments in that no one variety was most productive in any two years. It is this condition which makes still more striking the fact that Burr-Leaming yielded more than the most productive of the five varieties in 3 of the 5 years. In the entire period Burr-Leaming yielded 18 bushels (27.5 per cent) more than the average of the varieties.

The results of later experiments at the Connecticut station also are of interest. The yields of combinations between lines of Century and Leaming after four generations of selfing and selection, as reported by Jones and Mangelsdorf (*43*) are shown in Table 7. The yields of the parent varieties, which are among the higher yielding varieties under the conditions of the experiment, are shown for comparison.

In these experiments, although the yields of the single crosses exceeded those of their respective parent varieties but slightly, the double cross yielded 22.3 bushels (47 per cent) more than Century, the higher yielding variety.

TABLE 7.—*Comparative yields of the Century and Leaming varieties of corn and of F_1 crosses and a double cross between selfed lines of these varieties in Connecticut*

[Data from Jones and Mangelsdorf (*43, p. 182*)]

Designation	Acre yields (bushels)
Century variety (110)	47.5
Leaming variety (112)	44.4
Single cross (110-2×110-4)	51.2
Single cross (112-1×112-4)	45.6
Double cross (110-2×110-4)×(112-1×112-4))	69.8

The results of extensive comparisons of crosses between selfed lines and the parent variety made at the Nebraska station have been reported by Kiesselbach (*48*). A summary of the data on crosses between selfed lines from the high-yielding stock of the Hogue variety is given in Table 8.

TABLE 8.—*Comparative yields of Hogue corn and of crosses between selfed lines of this variety at Lincoln, Nebr., in years stated*

[Data from Kiesselbach (*48, p. 53*)]

Designation	Acre yields of shelled corn (bushels)				
	1913	1915	1916	1917	Average
Crosses between selfed lines:					
4×12	22.0	61.9	38.8	60.6	45.8
4×1	26.8	64.8	53.2	41.6	46.6
12×5	22.8	69.5	44.6	48.5	46.4
8×2	20.1	71.3	66.2	51.9	52.4
12×2	21.9	73.6	58.0	59.4	53.2
10×12	22.7	57.9	51.5	53.6	46.4
10×5	24.2	61.0	43.3	51.0	44.9
2×10	25.6	75.4	58.2	45.2	51.1
Average	23.3	66.9	51.7	51.5	48.3
Original Hogue	11.4	73.1	34.5	46.0	41.2

The average yield of the crosses exceeded the yield of Hogue in three of the four years for which data are reported. Whether the failure of many of the crosses to yield more in 1915 was due to the fact that the crosses were adapted better to a lower level of productivity than obtained in that year is not known, though the data suggest such a possibility. Two of the crosses, however (12×2 and 2×10), yielded more than Hogue in each year, their average increase for the four years being 29.1 and 24 per cent, respectively. It is characteristic of experiments of this kind that the three leading crosses had a single line (No. 2) as one parent.

Kiesselbach (*48, p. 63*) also reports the yields of crosses between selfed lines selected from stocks of the Hogue variety having high leaf area and low leaf area. Of the 29 crosses for which data are reported, 20 yielded more and 9 yielded less than the parent variety, as an average for the years 1915 and 1916. The average acre yield of the 29 crosses was 60.2 bushels in comparison with 55.1 bushels for Hogue. It should be emphasized again that, although it is inter-

esting to note the high average yields of these crosses, the real importance attaches to those crosses that yield most. Thus, in these data, 5 crosses yielded more than 70 bushels per acre, the highest yield being 74.1 bushels, or 35.5 per cent more than Hogue.

Selection within selfed lines as a basis for corn improvement has been under trial at the Minnesota station for a number of years. The results of some of these experiments recently have been summarized by Hayes (*30, p. 351*) as follows:

> In 1924, of a total of 21 double crosses tested, 3 yielded less than the higher yielding commercial variety. One double cross exceeded the better commercial variety by 30 per cent. The 7 double crosses in which dent inbred strains were used yielded 13 per cent more on the average than the better variety, while 12 flint-dent crosses average 9 per cent more than the better variety. Of 2 flint double crosses one gave a low yield and the other yielded rather well. The results in 1925 were similar and certainly indicate that double crosses in which desirable appearing selfed lines are used may be expected to yield more than the present standard varieties.

The experiments at the Minnesota station also have included limited experiments with synthetic varieties through the F_2 generation. The results of these are given in Table 9.

TABLE 9.—*Yields of the F_2 generation of synthetic varieties and of the commercial parent varieties at University Farm, St. Paul, Minn., in 1925*

[After Hayes (*30, p. 352*)]

Designation	Selfed lines used in synthetic variety		Acre yields	
	Number of years selfed	Number of lines	Bushels	Increase above (+) or decrease below (−) parent variety (per cent)
Minnesota No. 13:				
Commercial			51.3	
Synthetic	1	5	45.3	−11.7
	3	3		
	8	1		
Rustler:				
Commercial			44.8	
Synthetic	1	2	47.5	+6.0
	2	7		
	3	5		
	4	3		
Northwestern Dent:				
Commercial			51.9	
Synthetic	1	2	60.5	+16.6
	3	8		
King Phillip:				
Commercial			40.3	
Synthetic	3	11	43.3	+7.4
Longfellow:				
Commercial			43.9	
Synthetic	3	8	40.1	−8.7

It should be emphasized that these data give the results of preliminary experiments to determine the possibilities in this method of utilizing selection within self-fertilized lines, not the yields of strains of known productiveness. In view of this fact the results are extremely promising.

The Delta Prolific variety of corn, originated by the Bureau of Plant Industry, has been among the higher yielding varieties in a number of varietal experiments in eastern Arkansas and in some

other Southern States. Increased yields obtained from crosses between selfed lines above the yield of this variety consequently represent approximately the superiority of these crosses over the best commercial varieties available for this section. Data on the yields of crosses between selfed lines of Delta Prolific in Arkansas and Tennessee have been reported (*63*, *64*). The superiority or inferiority of each of 74 crosses to Delta Prolific based on the yields at Knoxville, Tenn., in 1923 is shown in Table 10, the data being arranged to show strain tendencies.

Of the 74 crosses for which data are shown, 29 yielded more and 45 yielded less than the parent variety. The individuality of certain lines in crosses is very evident. Thus, crosses of three lines of 5-1- with 2-2-2-4-2-1 are slightly superior to the parent variety, whereas the same lines crossed with 2-2-2-4-4-1 produced decidedly inferior yields. The outstanding lines of the experiment are those of the 10-3-1 strain. Of the 74 crosses, 11 involved a line of 10-3-2- as one parent. Of the other 63, 26 yielded more and 37 yielded less than Delta Prolific. The value of 10-3-1- in hybrids is shown by the fact that it was one parent of 18 (69 per cent) of the superior crosses and of only 12 (32 per cent) of the inferior crosses. This is further evidence of the importance of selection on the basis of production in hybrid combinations, as the yields of the 10-3-1- selfed lines are not high.

Some of the better yielding combinations included in the experiments in Tennessee were grown in comparison with the parent variety at Burdette, in 1925, from crossed seed produced at Knoxville, Tenn., in 1924. The yields of these crosses as percentages of the yields of Delta Prolific grown in adjacent plats are given in Table 11. The yields of the same combinations as percentages of the yield of Delta Prolific grown in the same row at Knoxville, Tenn., are shown for comparison.

TABLE 10.—*Average yields of crosses between selfed lines of Delta Prolific corn above (+) or below (—) the comparable yield of the parent variety at Knoxville, Tenn., in 1923*

[Data from Richey and Mayer (*64*, *p. 14*)]

Pedigrees of parent lines	Increase above (+) or decrease below (—) acre yields of shelled corn of parent variety (bushels)											
	2-2-1-3-2-1	2-2-2-4-2-1	2-2-2-4-4-1	2-2-2-4-6-2 or 3	5-1-2-2-1-3	5-1-2-3-2-2	5-1-3-1-1-2	5-1-3-3-1-2	7-4-1-6-6-2	7-4-1-7-4-1	7-4-2-1-1-2	7-4-2-6-2-2
5-1-2-2-1-3	+1.3	+9.0	−29.8	------	------	------	------	------	------	------	------	------
5-1-2-3-2-2	−20.5	+3.4	−21.9	+ 4.0	------	------	------	------	------	------	------	------
5-1-3-1-1-2	−18.6	+.4	−13.6	−20.9	------	------	------	------	------	------	------	------
5-1-3-3-1-2	−36.9	------	------	−20.4	------	------	------	------	------	------	------	------
7-4-1-6-6-2	+2.1	------	+10.8	------	+2.6	------	−15.1	−6.1	------	------	------	------
7-4-1-7-4-1	−6.9	------	------	−13.1	−16.3	−17.0	−11.3	−6.6	------	------	------	------
7-4-2-1-1-2	−4.4	------	−5.6	------	------	−1.0	−14.8	------	------	------	------	------
7-4-2-6-2-2	------	−20.8	−8.3	−20.4	−1.8	------	------	−12.8	------	------	------	------
10-3-1-1-1-4	−18.1	------	−1.5	−1.5	−4.0	------	+6.4	+6.9	+15.4	------	------	−10.4
10-3-1-1-2-2	−6.1	+20.6	+30.0	+2.1	+15.8	+11.0	------	−8.3	+15.0	------	------	−6.4
10-3-1-2-1-4 or 5	------	+6.4	------	−8.6	------	------	+6.8	+3.9	+22.1	------	------	+2.5
10-3-1-2-2-3	+11.8	------	+10.4	------	+5.4	------	−6.8	−14.1	−6.8	------	+28.9	------
10-3-2-1-2-1	------	------	−2.1	+.1	------	------	−14.6	−8.0	------	−29.8	------	------
10-3-2-1-3-3	------	------	------	−18.8	------	−5.5	−7.9	−17.3	+5.5	+4.6	------	------

TABLE 11.—*Yields of crosses between selfed lines of Delta Prolific corn as percentages of comparable yields of the parent variety, obtained at Burdette, Ark., in 1925 and at Knoxville, Tenn., in 1923*

[Experiments at Burdette, Ark., were in cooperation with the Burdette Plantation (Inc.) and the Arkansas Agricultural Experiment Station. Data for Knoxville, Tenn., from Richey and Mayer (*64, pp. 12, 13*)]

Pedigrees of parent lines [1]		Acre yields of crosses compared with those of the parent variety (per cent)					
		2-2-2-4-4-1	2-2-2-4-2-1	5-1-2-2-1-3	5-1-2-3-2-2	7-4-1-6-6-2	7-4-2-1-1-2
5-1-2-2-1-3	Burdette	------	111	------	------	------	------
	Knoxville	------	112	------	------	------	------
5-1-2-3-2-2	Burdette	137	------	------	------	------	------
	Knoxville	70	------	------	------	------	------
10-3-1-1-1-4	Burdette	------	------	------	------	127	------
	Knoxville	------	------	------	------	134	------
10-3-1-1-2-2	Burdette	------	133	127	118	120	------
	Knoxville	------	129	120	117	121	------
10-3-1-2-1-5	Burdette	------	------	------	------	108	------
	Knoxville	------	------	------	------	137	------
10-3-1-2-2-3	Burdette	140	------	------	------	------	114
	Knoxville	114	------	------	------	------	154

[1] The pedigrees shown are for the lines used in the crosses at Knoxville, Tenn.; those for the lines used in the crosses at Burdette, Ark., would be the same with further numbers added.

With a single exception, for which no reason is known, the results are in fair agreement and indicate that increased yields ranging from 20 to 30 per cent could be obtained by using any one of several crosses. These crosses were all at a disadvantage because of the poor seed value due to the seed being produced on the weak plants of the selfed lines. In fact, none of the single crosses could be recommended for practical use because of danger of a poor stand should conditions be unfavorable for germination. This disadvantage is overcome by double crossing. So far the only data available on the yields of double crosses involving the selfed lines of Delta Prolific come from duplicate plats of a random mixture of double crosses included in the comparison at Burdette, Ark., in 1925. The two plats of the double crosses yielded 41.6 and 44.5 per cent more than the respective adjacent plats of Delta Prolific. Too much confidence should not be placed in the exact size of these increases obtained in a single experiment. At the same time they are of an order that is consistent with expectation based on the more extensive comparisons of the component single crosses.

The results of the Iowa corn-yield test conducted by the Iowa Corn and Small-Grain Growers' Association in cooperation with the Iowa Agricultural Experiment Station and the Bureau of Plant Industry of the United States Department of Agriculture provide further interesting evidence on the productiveness of crosses between selfed lines of corn. Any farmer in Iowa may enter his corn in this test upon payment of a small fee, and farmers outside of Iowa have the same privilege, though the fee is somewhat larger. The State is divided into four sections from north to south with an eastern, central, and western district in each section for the purposes of this test. Each variety entered is compared carefully for productiveness in one or more districts at the option of the farmer

entering it. Entries for the three districts of a section are known as "section entries," and the average productiveness of these entries on the three farms in the section is reported separately. The yields of the 10 leading section entries in the south-central section in 1924 and 1925, as published in the Annual Reports of the Iowa Yield Test (*1*, *66*), are given in Table 12.

TABLE 12.—*Yields of the 10 leading entries in the south-central section of the Iowa corn-yield test in 1924 and 1925*

[Adapted from Iowa investigators (*1*, *66*)]

1924			1925		
Rank	Designation	Acre yield (bushels)	Rank	Designation	Acre yield (bushels)
1	F_1 Hybrids [1]	51.33	1	Hybrid B [1]	77.13
2	Copper Cross [1]	45.11	2	Ioleaming [2]	77.05
3	Ioleaming [2]	41.18	3	Hybrid C [1]	73.81
4	Leaming×White Pearl [1]	40.30	4	Hybrid A [1]	70.94
5	Bloody Butcher×White Pearl [1]	40.21	5	Reid	69.81
6	Black's Reid	39.10	6	Black's Reid	69.57
7	Bass Yellow	38.80	7	——[3]	69.07
8	Krug	38.34	8	——[3]	68.33
9	Lemon Yellow	38.16	9	——[3]	68.07
10	Reid	38.00	10	——[3]	67.60

[1] Crosses between selfed lines.
[2] Cross between two strains of Leaming.
[3] Information is not reported, as entries ranked below the top third.

The first five ranking entries in 1924 and the first four ranking entries in 1925 were crosses. One cross in each year was between open-fertilized strains, and the others were between selfed lines. With the exception of the entry ranking first in 1924, which was entered by the Bureau of Plant Industry, all of the crosses were entered by private individuals. Of most interest, however, are the outstanding yields of the best crosses above those of the best commercial varieties, the superiority being 31.3 per cent in 1924 and 10.5 per cent in 1925.

Summarizing the preceding data, it may be said that (1) in all of the experiments some cross or crosses have been significantly higher yielding than the best commercial varieties available for the sections where the comparisons have been made; (2) the increases obtained from the more productive crosses have been large, many of them being 30 per cent or more; (3) when the same crosses have been compared over a series of years, the results from season to season have been consistent enough to show that the larger yields from the crosses could be expected to follow with reasonable assurance; and (4) consistency also is shown by the performance of several crosses of similar parental constitution.

PLACE OF SELECTION WITHIN SELFED LINES

The methods of reproduction and inheritance in corn which were considered in the first part of this bulletin show clearly that controlled pollination is the only basis for definite corn breeding. They also suggest a period of self-fertilization as the desirable initial step in such a program, in order that lines breeding true for various

characters may be isolated for use as selection stocks. It has been abundantly proved that strains can be obtained in this way which breed true for differences in physiologic functioning in relation to temperature (*17*), moisture (*49*), and soil nutrient requirements (*31*), as well as for those conditions or processes which may determine the difference between resistance and susceptibility to various disease organisms (*33*). Finally, the yields of crosses between selfed lines so far reported show conclusively that increased acre yields of corn ranging from 20 to 30 per cent or more can be obtained in many cases. The comparisons have not been as extensive as they might be. Nevertheless, taken in connection with the soundness of the underlying theory, they have been striking enough and consistent enough to establish selection within selfed lines as the basis for present-day methods of corn improvement.

Breeding corn by selection within selfed lines always will be experimental. Only a few of the lines or combinations resulting from the breeding program will represent improvement, and these will have to be determined by experiment. Consequently, breeding by selection within selfed lines is primarily for the trained plant breeder working at the State agricultural experiment stations or with associations of farmers or with seedsmen. Few farmers have the time or facilities to devote to the intensive and extensive labor of hand pollinating and testing over a period of years that is required for a comprehensive corn-improvement program of this kind. Occasional individuals having the means and inclination may find corn breeding by these methods an interesting and possibly a profitable occupation. They will be the exception. The real burden of finding the best combinations will and should fall on the agricultural experiment stations. These agencies have the necessary facilities for selecting the lines and for comparing the crosses carefully so as to insure that only those which really are superior are distributed for commercial use.

The function of the farmer will be in the annual production of crossed seed of combinations that have been shown to be superior. A number of essentials are involved in successfully maintaining the individual lines, crossing them in one way or another, and insuring that the seed produced is of good quality and germination. Reserve stocks of the selfed lines must be maintained to guard against crop failure. There must be no question as to which lines or crosses are which, either in storage or in the field. Tassels must be removed from all pistillate parent plants before they have shed any pollen. Finally, the commercial seed must be harvested and handled at a time and in a way to insure that it will retain its full vigor of germination. The successful accomplishment of these essentials requires an uncommon willingness and ability to do the right thing at the right time. To those who have this willingness and ability the commercial production of seed of crosses between selfed lines should offer an attractive and remunerative field just as soon as combinations that are outstanding for their localities are available.

The methods of corn improvement based on selection within selfed lines should be recognized as still in an experimental stage. Little is known as to what makes some lines yield more in crosses than others. Consequently the better lines must be determined largely by

trial in hybrid combination. This takes time and decreases the likelihood of obtaining the best possible combinations. There also is little evidence as to the relative value of single crosses, double crosses, and synthetic varieties for commercial utilization and practically none as to the possibility of obtaining lines that are themselves high yielding. Much remains for the future. In the meantime the utilization of the facts already learned will permit an increase in the acre yield of corn on many farms just as soon as high-yielding crosses between selfed lines that are adapted to the various sections of the country can be found and as soon as practical methods for producing and distributing seed of such crosses annually can be developed.

DISCUSSION

So-called varieties of corn really are complex mixtures of hybrids. They can be modified easily and quickly up to a certain point by mass selection. If mass selection is effective at all beyond this point, progress is so slow that the results can not be demonstrated from year to year. Nearly all of the present varieties of corn have been adapted by mass selection to the widely different conditions under which they are grown. The productiveness of many of them can be further increased by careful selection of seed from normal, vigorous, productive plants of a type adapted to the specific environment. The same means may be relied upon to maintain the productiveness of varieties which already have reached the approximate limits of improvement by mass selection. This kind of breeding is a proper function of the farmer who grows his own seed corn or who may specialize in seed corn for sale. It also is the only kind of corn breeding which most farmers are justified in undertaking.

Ear-to-row selection was suggested as a marked improvement over mass selection on the basis of theoretical considerations. The soundness of the underlying theory, in so far as it is sound, has been shown repeatedly by the larger yields obtained from the immediate progenies of higher yielding parent ears. Ear-to-row selection failed as a means of increasing commercial production chiefly because mass selection was more nearly its equal in efficiency than had been thought to be the case. Ear-to-row selection was concerned only with hybrids, the methods followed being planned carefully to maintain a high degree of hybridity. As a consequence, the productiveness of the best progenies was only that of hybrid mixtures averaging better than the mixture which constituted the variety as a whole. Maximum yields were prevented by the poorer components of these mixtures. Furthermore, nothing was fixed. Even the larger yield frequently obtained from the immediate progeny of a more productive parent ear was lost during the segregation and recombination that took place while the seed was being multiplied for commercial utilization. It is barely possible that special cases will exist in which the use of ear-to-row selection may be justified. In view of the labor and expense involved and its negligible advantages over mass selection, however, ear-to-row selection can not be recommended as a general method.

Many F_1 crosses between varieties of corn have yielded more than the average of their parents and some have yielded more than the better parent. The only varietal crosses that are of value commer-

cially, however, are those which are more productive than the best varieties available, and the proportion of such crosses has been relatively small. Crossing varieties of corn at random can not be recommended as a means of obtaining maximum yields. The superior combinations must be determined by careful experiment over a period of years. Even then there usually is no assurance that this superiority will be maintained, as the parent varieties themselves are but mixtures of hybrids and therefore grossly unstable. Varietal crossing may have a place in obtaining larger yields of corn when the object is to bring into expression in a single stock favorable dominant characters from each of two varieties. Thus, there is some evidence that the partial dominance of quick maturity in small-growing varieties and of larger size in sorts that require a longer season to mature may both be expressed in the crosses between these types. If so, such crosses might have an important place near the northern limits of corn production. Aside from such special cases, however, the use of F_1 varietal crosses seems to offer little that is practical in the way of corn improvement.

Selection within selfed lines is a genetically sound basis for corn improvement, and it is by methods involving selection within selfed lines that corn breeders of to-day are attempting to obtain materially larger acre yields of corn. Preliminary results of these attempts indicate that crosses or double crosses between selfed lines can be used to obtain consistent increases of 20 to 30 per cent or more above the acre yields of the best present varieties.

The crossed seed from which the large yields are obtained must be grown each year, and farmers using such seed would have to obtain a new supply either by purchase or by growing it themselves in special seed plats. This involves difficulties in seed production and distribution that must be overcome if crossed seed is to be used on a large scale. Seedsmen will be able to supply part of the demand. If the purchase of seed became at all general, however, only a small part of the approximately 20,000,000 bushels of seed corn that is used in the United States annually could be supplied through existing commercial channels. Individual farmers in different sections could specialize in the production of crossed seed for sale. It also seems probable that groups of farmers could combine for the purpose of producing enough crossed seed for their own use. These are only suggestions. The best methods will be worked out only when crosses of high productiveness are known and the demand for seed of them is created. There is little doubt that ways will be found to meet the demand when it exists.

Before the better methods of producing and distributing crossed seed can be determined, high-yielding crosses must be found for various sections of the United States. Very few crosses as yet have been tested thoroughly enough to warrant their recommendation for commercial planting. Experimental corn breeding involving selection within selfed lines is being conducted by the specialists of the Bureau of Plant Industry and of most of the State agricultural experiment stations. Not only are attempts being made to find lines which will produce high-yielding crosses, but different methods of utilizing selfed lines are being compared and studies are being made of the factors that cause lines to be good or poor in the selfed condi-

tion or in combination. As a result of these experiments it is highly probable that crosses between selfed lines will be found that can be utilized to produce larger acre yields of corn in the different States. It is not improbable that other methods for utilizing selfed lines that are being tried now or that may suggest themselves later will be found more practical for commercial utilization than crosses or double crosses. In any event it will be some time before even high-yielding single crosses are available for most sections of the United States. At least three or four years of self-fertilizing are necessary before crosses can be made for preliminary testing, which requires another year. Another season is used in recrossing the lines indicated as promising by the preliminary trial in order to obtain seed for a more thorough comparison. It consequently requires six or seven years to locate the few better crosses that are worthy of more extensive comparison under more nearly practical conditions. Even more time is needed if double crosses or synthetic varieties are to be found. It evidently will be some time, therefore, before these products of the newer methods of corn breeding can come into anything like general use.

It is advisable to insert a word of caution as to buying crossed seed corn. The large yields that have been obtained experimentally from some crosses are likely to create a demand for crossed seed before it can be supplied in any considerable quantity. This will make it possible to obtain a large price for the supplies that do exist. There is no objection to a reasonably high price for seed corn that will yield 10 to 15 bushels per acre more than the best present varieties. One bushel of such seed will increase the income about $30 to $45, assuming that it will plant 6 acres and that corn is worth 50 cents a bushel. Unfortunately, there are likely to be many individuals who will offer to sell crossed seed at a large price when the seed is little, if any, more productive than ordinary seed corn. Either the absolute honesty of the one offering crossed seed for sale must be known to the buyer or the latter must realize that he is taking chances of being defrauded. The greatest danger from fraud of this kind will exist before crossed seed is available generally through the ordinary channels. Methods of seed inspection and certification presumably will be developed later that will restrict effectually the opportunities for dishonesty. In the meantime farmers should be particularly cautious about buying seed for which extravagant claims are made by people of unknown standing.

Furthermore, it should be recognized that adaptation is just as important a factor in determining the yield of crosses as it is in determining the yield of varieties. That a cross is unusually productive in one section is no evidence that it can be grown profitably in another locality with a different environment. Consequently if a farmer wishes to buy seed of a cross because it has yielded unusually well elsewhere he should buy only a small quantity at first and recognize that it is an experiment. If planted on a large scale he may lose considerably either by the cross yielding poorly under his conditions or by its failing to mature properly, or by both.

In conclusion, it may be said that selection within selfed lines unquestionably offers opportunities for obtaining materially larger acre yields of corn. Methods involving this principle are primarily

for the specialized plant breeder in so far as isolating lines that produce the high-yielding crosses is concerned. The function of the farmer will be in producing seed for commercial planting of those combinations that have been proved to be high yielding. Selection within selfed lines still is in an experimental stage and its benefits will not be available generally for some years. In the meantime advantage should be taken of whatever crosses may be proved to be more productive in the different sections. By mass selection the yields of the better existing varieties may be maintained and possibly increased. Mass selection primarily is the method for the farmer to use in producing either his own seed corn or seed corn for sale. Moreover, it is the only method that can be recommended for the use of the farmer at the present time. Between careful mass selection on the one hand and selection within selfed lines on the other, no method of corn breeding that has been tried has offered enough advantage to warrant its recommendation.

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